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UTILISATION DES ISOTOPES STABLES DE L'AZOTE DANS L'ÉTUDE DE L'IMPACT DES ACTIVITÉS HUMAINES SUR LA STRUCTURE DES COMMUNAUTÉS AQUATIQUES

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RÉSUMÉ

La perturbation du cycle de l'azote et l'altération de la structure des communautés aquatiques sont deux conséquences de l'intensification des activités humaines (agriculture, développement résidentiel, foresterie, industries, etc.) à l'échelle des bassins versants. L'augmentation des concentrations de nutriments dans les milieux aquatiques accroît la productivité de ces systèmes et accélère leur eutrophisation, tandis que l'accroissement des concentrations de contaminants industriels élimine diverses espèces d'organismes sensibles à ce type de pollution. Dans ce document, nous examinons l'utilité des signatures isotopiques de l'azote ($\delta^{15}N$) en tant qu'indice de la structure des communautés dans des rivières touchées par différents types et intensités d'activités anthropiques. Nous examinons également comment le $\delta^{15}N$ des organismes aquatiques peut être utilisé en tant qu'indicateur de la perturbation du cycle de l'azote par les activités humaines à l'échelle des bassins versants.

La présente étude révèle premièrement que le $\delta^{15}N$ des invertébrés aquatiques et des poissons est fortement corrélé aux charges totales en azote anthropique produites dans le bassin versant, ainsi qu'aux charges provenant respectivement du fumier animal, des fertilisants chimiques et de la population humaine. Dans l'ensemble, ces résultats suggèrent que l'azote lié aux activités anthropiques se retrouve dans les milieux aquatiques et est assimilé par les organismes qui y vivent. Ils suggèrent ainsi que le $\delta^{15}N$ des consommateurs aquatiques peut être utilisé comme indicateur des quantités d'azote anthropique qui se retrouvent en milieu aquatique. Ces résultats montrent également à quel point le $\delta^{15}N$ des organismes est variable dans l'espace. Voilà une première raison pour laquelle le développement d'une méthode de calcul de la position trophique des organismes lotiques s'avérait nécessaire. Une seconde raison appuyant le développement d'une méthode particulière de calcul est que le $\delta^{15}N$ de différents groupes de consommateurs primaires est significativement différent à l'intérieur d'un même site. Ainsi, ce n'est pas n'importe quel consommateur primaire qui peut servir d'organisme de référence, certains consommateurs étant plus omnivores que d'autres. Dans les rivières examinées, les brouteurs furent identifiés comme des organismes de référence adéquats et furent utilisés afin d'estimer la position trophique des consommateurs aquatiques. Les brouteurs présentaient effectivement des valeurs de $\delta^{15}N$ faibles (témoignant de leurs habitudes alimentaires peu carnivores) et étaient bien répartis entre les sites d'étude. Le principal constat de ce volet est qu'il vaut mieux, lors du calcul de la position trophique des organismes lotiques, sélectionner en tant qu'organismes de référence un nombre restreint de types d'organismes qui partagent des habitudes alimentaires peu omnivores (les plus herbivores possibles) et similaires entre les différents sites d'étude.

Les isotopes stables de l'azote peuvent aussi fournir certaines informations sur la structure des communautés aquatiques et comment celles-ci sont influencées par les activités anthropiques. Premièrement, les positions trophiques des organismes

lotiques estimées à l'aide du $\delta^{15}N$ correspondaient, de façon générale, à celles présentées dans la littérature. La position trophique moyenne se chiffrait à 2,3 pour les consommateurs primaires, à 2,9 pour les invertébrés prédateurs et à 3,5 pour les poissons se nourrissant d'invertébrés. La position trophique semble donc dresser un portrait réaliste du comportement alimentaire des organismes. Toutefois, la position trophique des poissons s'avérait trop influencée par le comportement alimentaire de ces derniers (préférences alimentaires) pour refléter les changements dans la structure trophique de la communauté d'invertébrés dont se nourrissent les poissons. En effet, la position trophique des poissons n'était pas liée à la présence de prédateurs dans le réseau trophique et n'était pas influencée par la productivité (chlorophylle *a* dans l'eau) ou les perturbations (nombre d'industries sur le bassin versant). À l'inverse, les pentes $\delta^{15}N$-taille des communautés d'invertébrés répondaient de façon significative à la présence de prédateurs, ainsi qu'à la productivité et aux perturbations. Plus précisément, les pentes $\delta^{15}N$-taille étaient plus élevées dans les sites productifs et contenant une plus forte proportion de gros prédateurs et moins élevées dans les sites perturbés. Ces observations suggèrent notamment que la longueur des chaînes alimentaires, dont les pentes $\delta^{15}N$-taille sont un indice, est altérée par les activités humaines. Finalement, la position trophique moyenne des classes de taille de la communauté d'invertébrés, bien que significativement variable entre les sites d'étude, n'expliquait pas les changements enregistrés dans la densité des invertébrés (à l'intérieur de ces mêmes classes). De plus, la densité n'était que faiblement positivement corrélée à la productivité du milieu (chlorophylle *a*). L'effet des facteurs examinés pourrait être obscurci par d'autres facteurs tels que la prédation, le type d'habitat ou la pollution anthropique.

En somme, les isotopes stables de l'azote s'avèrent de bons indicateurs de la présence d'azote d'origine anthropique dans les cours d'eau et de la perturbation du cycle de l'azote par les activités anthropiques à l'échelle des bassins versants. Ils permettent aussi d'estimer rapidement la position trophique des organismes et offrent une information réaliste sur le comportement alimentaire de ces derniers. Ils permettent également de décrire, dans une certaine mesure, la structure trophique des chaînes alimentaires (en particulier pour ce qui est des pentes $\delta^{15}N$-taille) et comment celles-ci sont altérées par les activités anthropiques.

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INTRODUCTION GÉNÉRALE ET REVUE DE LA LITTÉRATURE

Les relations trophiques entre les organismes vivants et les facteurs régissant la structure des réseaux trophiques auxquels ces derniers appartiennent sont des sujets qui ont intéressés de nombreux chercheurs. Déjà au début du XX^{e} siècle, Lindeman (1942) et Elton (1971 (première version en 1927)) s'interrogeaient sur la nature des relations entre les organismes dans la nature. Dans ses travaux, Lindeman propose même un schéma représentant un réseau trophique lacustre, illustrant les nombreux liens possibles entre les différents consommateurs qui le composent. Ces premières interrogations seront cristallisées par la publication de l'étude de Hairston et al. (1960), qui jette les bases théoriques sur les facteurs qui régulent les populations d'organismes. Ces derniers proposent que les organismes vivants sont soit limités par les ressources disponibles (nourriture), soit contrôlés par la prédation. Cette réflexion donne naissance à de nombreuses études et théories subséquentes qui cherchent à élucider les facteurs régissant les populations animales et végétales, ainsi que la longueur des chaînes alimentaires auxquelles elles appartiennent (Fretwell 1977; Oksanen et al. 1981; Abrams 1993, entre autres).

Parmi les facteurs examinés, la productivité du milieu et la présence de perturbations environnementales ou anthropiques seraient deux facteurs qui auraient un effet déterminant sur les chaînes alimentaires. L'hypothèse concernant la productivité propose qu'un système plus productif sera en mesure de supporter de plus longues chaînes alimentaires qu'un système peu productif (Fretwell 1977; Oksanen et al. 1981). Ceci serait dû au fait qu'une plus grande productivité équivaut à une plus grande quantité d'énergie disponible à la base de la chaîne alimentaire. Cette énergie permettrait de supporter de plus vastes populations de consommateurs primaires qui, à leur tour, pourraient supporter de plus grandes populations de consommateurs secondaires, puis tertiaires. À l'inverse, l'hypothèse portant sur l'effet des perturbations suggère qu'il y aurait une réduction de la longueur des

chaînes alimentaires dans les systèmes perturbés (Odum 1985; Menge et Sutherland 1987). En effet, plusieurs études ont démontré que de nombreux taxons sensibles aux perturbations (pollution, sécheresse, etc.) disparaissent des milieux affectés (Ford 1989; Jenkins et al. 1992; Quinn et Hickey 1993). En particulier, certains gros invertébrés prédateurs semblent particulièrement vulnérables aux perturbations (Resh et al. 1996; Voshell 2002). La disparition de tels organismes, qui peuvent représenter des maillons importants dans la chaîne alimentaire, aurait donc pour effet de rétrécir cette dernière.

Les activités humaines seraient susceptibles d'altérer la structure des réseaux trophiques lotiques, puisque celles-ci modifient la productivité des écosystèmes aquatiques et s'avèrent également être une source de perturbation. Premièrement, les rejets agricoles et urbains sont souvent une source importante de nutriments (azote et phosphore) qui sont exportés vers les milieux aquatiques (Chambers et al. 2001; Rabalais 2002). Considérant que l'azote et le phosphore sont des nutriments qui favorisent la croissance des producteurs primaires (plantes et algues), une importante source de nourriture à la base des chaînes alimentaires aquatiques, on peut croire que les activités humaines augmentent la productivité des écosystèmes aquatiques. En second lieu, les rejets industriels représentent une perturbation du milieu aquatique, via le déversement de contaminants qui peuvent s'avérer toxiques pour plusieurs espèces d'organismes aquatiques (Wiederholm 1984; Hellawell 1986; Ford 1989).

Conséquemment, on pourrait premièrement s'attendre à un allongement de la chaîne alimentaire dans les milieux touchés par des rejets de nutriments d'origine anthropique. Plusieurs études ont d'ailleurs observé de plus longues chaînes alimentaires dans les milieux plus productifs (Jenkins et al. 1992; Townsend et al. 1998; Thompson et Townsend 2005). Toutefois, d'autres études ont noté une diminution de la richesse spécifique et une simplification des réseaux trophiques dans les sites productifs (Dance et Hynes 1980; Harding et al. 1998; Harding et al. 1999).

Cette seconde observation suggère qu'une forte productivité pourrait constituer davantage une source de perturbation qu'une réelle source productivité. Cette hypothèse est appuyée par les travaux de Persson et al. (1992), qui ont observé une relation en forme de dôme entre la longueur des chaînes alimentaires en lacs et la productivité (chlorophylle *a*). Ainsi, on pourrait donc s'attendre à un allongement de la chaîne alimentaire en premier lieu, avec l'accroissement de la productivité, suivi en second lieu d'un rétrécissement de la chaîne au fur et à mesure que la productivité continue de s'élever. Deuxièmement, on pourrait s'attendre à observer de courtes chaînes alimentaires dans les milieux touchés par des rejets de contaminants d'origine industrielle. Plusieurs auteurs ont noté une perte de biodiversité dans des milieux aquatiques affectés par des rejets de substances provenant d'activités industrielles (Garie et McIntosh 1986; Ford 1989; Sibley et al. 2000; Pelletier 2002), perte qui pourrait se traduire en une diminution de la longueur des chaînes. D'ailleurs, Sherwood et al. (2002) ont observé une simplification des chaînes alimentaires dans des lacs affectés par des contaminants. Ils ont découvert, en particulier, que cette simplification engendrait des répercussions importantes sur la croissance de poissons situés plus haut dans la chaîne alimentaire (perchaudes (*Perca flavescens*)).

Outre leur effet sur la longueur des chaînes alimentaires, les activités humaines peuvent indure d'autres types de changements dans les communautés. Ainsi, plusieurs études ont observé des changements dans la densité de divers types d'organismes en présence de rejets d'eaux usées urbaines, de rejets agricoles et industriels (Mayack et Waterhouse 1983; Garie et McIntosh 1986; Harding et al. 1999; deBruyn et al. 2003, par exemple). De façon globale, les milieux productifs semblent supporter de plus grandes densités d'invertébrés aquatiques que les milieux moins productifs (Hart et Robinson 1990; Sardá et al. 1996; Perrin et Richardson 1997). D'ailleurs, plusieurs études réalisées sur le terrain ont noté une augmentation des densités d'invertébrés dans des cours d'eau situés en milieu agricole (Corkum 1990; Manel et al. 2000; Harding et al. 1999). À l'inverse, certaines études ont

observé une diminution de la densité d'invertébrés dans des sites affectés par des rejets industriels et urbains ou par des rejets de pesticides en milieu agricole (Mayack et Waterhouse 1983; Dewey 1986; Garie et McIntosh 1986; Pelletier et St-Onge 1998), ce qui suggère que les substances toxiques associées à ces activités réduisent la densité d'organismes aquatiques. Les activités anthropiques ne sont pas les seuls facteurs à influencer la densité des organismes aquatiques. La température de l'eau, par exemple, peut favoriser une croissance plus rapide des invertébrés et favoriser une meilleure qualité et une plus grande quantité de nourriture à la base de la chaîne alimentaire (Cummins et Klug 1979; Sweeney 1984; Cossins et Bowler 1987; Gillooly et al. 2001). La position trophique des organismes pourrait aussi avoir un impact sur leur densité. En effet, selon la théorie sur l'efficacité de transfert de l'énergie chez les organismes vivants (Lindeman 1942; Slobodkin 1963; Kerr et Dickie 2001), les prédateurs devraient présenter des densités inférieures aux herbivores de même taille. Ceci serait dû au fait que le transfert de l'énergie vers le sommet de la chaîne alimentaire devient de moins en moins efficace au fur et à mesure qu'on s'élève dans cette chaîne. Conséquemment, il est plus difficile pour un prédateur d'obtenir des quantités suffisantes d'énergie pour survivre comparativement à un herbivore, ce qui diminue généralement la densité de prédateurs dans la nature.

Malgré la grande quantité d'études portant sur l'effet de facteurs environnementaux et humains sur la structure des communautés aquatiques, la plupart des résultats observés demeurent contradictoires. De plus, les outils traditionnellement utilisés pour examiner la structure des communautés présentent maintes lacunes. Premièrement, plusieurs études antérieures se sont limitées à de simples descriptions des communautés basées sur des longueurs de chaînes discrètes qui sous-estiment l'omnivorie (Oksanen et al. 1981; Persson et al. 1992; Abrams 1993). À l'inverse, d'autres études, plus complètes, ont exigé des efforts d'échantillonnage et d'identification importants afin de dépeindre un portrait réaliste

des chaînes alimentaires (études de connectance ou de contenus stomacaux : Briand et Cohen 1987; Spencer et Warren 1996; Townsend et al. 1998; Thompson et Townsend 2005). À titre d'exemple, les indices d'intégrité biotique ont été élaborés afin d'étudier l'impact de certains polluants sur la présence ou l'absence de taxons sensibles à la pollution (Resh et al. 1996). Toutefois, la compilation de ces indices nécessite une identification des organismes collectés qui s'avère parfois longue et exhaustive. Aussi, les résultats obtenus ciblent certains taxons indicateurs en particulier et ne permettent pas nécessairement de comprendre des processus complexes tels que les flux d'énergie dans la chaîne alimentaire ou la structure trophique réelle de la communauté.

Les isotopes stables de l'azote ($\delta^{15}N$) se présentent comme un outil permettant de mesurer rapidement la longueur d'une chaîne alimentaire et d'évaluer la structure des communautés et ce, en tenant compte de phénomènes complexes tels que l'omnivorie. La mesure des longueurs de chaînes à l'aide de la signature isotopique de l'azote est réalisable grâce au processus de fractionnement isotopique présent entre les organismes (Peterson et Fry 1987; Robinson 2001). Ce fractionnement se traduit par une hausse progressive du $\delta^{15}N$ (3,4‰ en moyenne) entre une proie et son prédateur immédiat (Minagawa et Wada 1984; Post 2002), qui est causée par une excrétion préférentielle des isotopes légers (^{14}N) par les organismes. Ainsi, un prédateur sera systématiquement enrichi par rapport à sa proie. Le $\delta^{15}N$ d'un consommateur augmente donc parallèlement à sa position trophique, ce qui permet de mesurer le nombre de niveaux trophiques présents entre ce dernier et un organisme situé à la base de la chaîne alimentaire (Cabana et Rasmussen 1994; Vander Zanden et al. 1997; Post 2002). Dans le présent document, nous employons la position trophique des consommateurs comme mesure de la longueur des chaînes alimentaires. La position trophique d'un consommateur est mesurée en soustrayant son $\delta^{15}N$ par

celui d'un organisme situé à la base de la chaîne alimentaire (soit un consommateur primaire, que l'on nommera « organisme de référence »), suivant la formule:

$$\text{Position trophique}_{\text{consommateur}} = [(\delta^{15}N_{\text{consommateur}} - \delta^{15}N_{\text{référence}}) / 3{,}4‰] + 2$$

où $\delta^{15}N_{\text{consommateur}}$ et $\delta^{15}N_{\text{référence}}$ représentent respectivement le $\delta^{15}N$ du consommateur pour lequel on souhaite estimer la position trophique et le $\delta^{15}N$ de l'organisme de référence. La valeur 3,4‰ représente le niveau moyen de fractionnement par niveau trophique, tandis que la valeur +2 correspond à la position trophique de l'organisme de référence (un herbivore) par rapport à la ressource de base, soit les nutriments. Ainsi, la position trophique du consommateur est mesurée par rapport à la ressource de base.

La raison pour laquelle le $\delta^{15}N$ d'un organisme de référence doit être soustrait du $\delta^{15}N$ du consommateur étudié est que le $\delta^{15}N$ est spatialement très variable. Le $\delta^{15}N$ brut d'un consommateur ne peut donc pas être utilisé seul afin d'estimer sa position trophique. Plusieurs études ont effectivement observé de fortes variations dans les valeurs de $\delta^{15}N$ entre différents sites d'étude (Hebert et Wassenaar 2001; Lake et al. 2001; Udy et Bunn 2001). En particulier, l'objectif de ma maîtrise (Anderson 2003) consistait à établir un lien entre les utilisations des terres et la signature isotopique de l'azote des organismes lotiques. Nous avons observé que le $\delta^{15}N$ était spatialement très variable et fortement corrélé au pourcentage d'agriculture pratiquée dans le bassin versant (Anderson et Cabana 2005). Quelques études ont également démontré que les charges d'azote associées aux diverses activités anthropiques pratiquées au sein des bassins versants généraient d'importantes variations dans le $\delta^{15}N$ de l'azote inorganique et des organismes aquatiques (McClelland et al. 1997; Mayer et al. 2002; Cole et al. 2004). Ces résultats suggèrent que les activités humaines pratiquées au sein des bassins versants perturbent le cycle

de l'azote (en générant des excédants d'azote dans les bassins versants et en accélérant leur écoulement vers les milieux aquatiques) et que cette perturbation peut être retracée jusque dans les chaînes alimentaires aquatiques. Cela signifie que les isotopes stables de l'azote, en plus de permettre de mesurer les longueurs de chaînes alimentaires en milieu aquatique (positions trophiques), pourraient potentiellement servir d'indicateurs des perturbations anthropiques du cycle de l'azote dans les bassins versants. Ils pourraient, en outre, servir de traceurs potentiels des diverses sources d'azote anthropiques en milieu aquatique.

Une autre utilisation possible des isotopes stables d'azote serait dans l'étude des relations entre le $\delta^{15}N$ et la taille des invertébrés à l'échelle de la communauté entière. Ces relations constitueraient un second outil permettant de mesurer rapidement la structure des communautés aquatiques (donc la longueur des chaînes alimentaires). La méthode consiste à rassembler les organismes par classe de taille, peu importe leur affiliation taxonomique, de mesurer le $\delta^{15}N$ de chaque classe de taille, puis d'examiner comment varie le $\delta^{15}N$ de la communauté entière en fonction de la taille. Elle permet aussi d'examiner la position trophique de chacune des classes de taille (reflétant des compartiments distincts d'un réseau trophique) et d'examiner les corrélations présentes entre ces différentes classes. En somme, cette approche, dite ataxonomique, permet de dépeindre un portrait global des interactions trophiques dans la communauté (flux d'énergie) sans cibler une espèce en particulier. Elle permet donc d'illustrer la façon avec laquelle l'ensemble de la communauté (du point de vue des interactions trophiques) répond à des facteurs environnementaux. Par exemple, une communauté d'invertébrés caractérisée par une proportion de plus en plus grande de gros prédateurs (augmentation du pourcentage de prédateurs avec la taille; présence de gros prédateurs se nourrissant de prédateurs moyens, qui s'alimentent eux-mêmes de petits prédateurs, etc.) devrait se refléter par un accroissement de plus en plus important du $\delta^{15}N$ avec la taille, puisque les prédateurs

ont un niveau trophique ($\delta^{15}N$) plus élevé que les autres organismes. À l'inverse, il ne devrait pas y avoir d'augmentation importante du $\delta^{15}N$ avec la taille dans une communauté où les invertébrés prédateurs sont absents. Comme les activités humaines sont susceptibles d'altérer la composition des communautés (effet sur la présence d'invertébrés prédateurs en particulier), ces dernières devraient également modifier la position trophique de chaque classe de taille et, conséquemment, influencer les relations $\delta^{15}N$-taille.

La présente thèse comprend quatre chapitres qui répondent à diverses interrogations soulevées dans le cadre du processus d'évaluation de l'impact des activités humaines sur la structure des communautés aquatiques. Le premier chapitre vise à mieux cerner la variabilité spatiale du $\delta^{15}N$ sur le territoire à l'étude ainsi que les facteurs anthropiques qui contribuent à cette variabilité. On y voit que le $\delta^{15}N$ des consommateurs aquatiques est fortement influencé par les charges anthropiques d'azote générées dans les bassins versants. Ce chapitre propose que le $\delta^{15}N$ des consommateurs aquatiques est un indicateur efficace de la perturbation du cycle de l'azote à l'échelle des bassins versants (c'est-à-dire, un traceur de l'écoulement des surplus d'azote produits dans le bassin versant et de leur assimilation dans les chaînes alimentaires aquatiques). Le chapitre 1 sert également d'introduction au chapitre 2, puisqu'il montre que le $\delta^{15}N$ est spatialement très variable, démontrant ainsi l'importance de corriger le $\delta^{15}N$ de tout consommateur pour lequel on veut estimer la position trophique par le $\delta^{15}N$ d'un organisme de référence. Le second chapitre amorce une réflexion sur les façons de calculer la position trophique des organismes et développe une méthode qui servira à estimer la position trophique d'organismes récoltés dans différentes rivières caractérisées par des $\delta^{15}N$ variables. Il présente aussi des estimations de la position trophique de nombreux consommateurs lotiques, basées sur la méthode développée, et compare ces dernières à celles présentées dans la littérature traditionnelle. Les troisième et quatrième chapitres, quant à eux, examinent

plus en profondeur l'impact de facteurs environnementaux et humains sur la structure des communautés aquatiques. En particulier, le troisième chapitre examine l'effet de trois facteurs ascendants sur la densité des communautés d'invertébrés lotiques. Il évalue plus précisément la capacité de la productivité, de la température et de la position trophique (estimée avec les isotopes stables de l'azote) à prédire la densité des communautés lotiques. Le chapitre 4, quant à lui, examine l'impact des perturbations d'origine anthropique et de la productivité sur la structure trophique des communautés aquatiques évaluée à l'aide des isotopes stables de l'azote (position trophique et pente δ^{15}N-taille). Au total, les chapitres constituant la présente thèse visent trois objectifs généraux: 1) l'évaluation des isotopes stables de l'azote comme traceurs des perturbations anthropiques du cycle de l'azote (et variabilité spatiale); 2) l'évaluation des isotopes stables de l'azote comme indicateurs de la structure des communautés; 3) l'étude de l'impact de facteurs environnementaux et anthropiques sur la structure des communautés aquatiques. Une brève introduction des quatre chapitres est présentée dans les paragraphes qui suivent.

Chapitre 1 : Le δ^{15}N des réseaux trophiques lotiques reflète-il la quantité et l'origine des charges d'azote provenant du bassin versant?

Les activités humaines ont grandement altéré le cycle global de l'azote (Vitousek et al. 1997; Tilman 1999; Galloway et Cowling 2002). En effet, les quantités d'azote associées aux pratiques humaines et atteignant les milieux aquatiques ont considérablement augmenté depuis les années 1950, accélérant l'eutrophisation de nombreux lacs et rivières (Vitousek et al. 1997; Howarth et al. 2002; Rabalais 2002). En particulier, les fertilisants chimiques, le fumier animal et les eaux usées figurent parmi les principales sources d'azote recensées dans les milieux aquatiques dans le monde (Vitousek et al. 1997; Howarth 1998; Green et al. 2004).

Quelques études antérieures ont révélé que les signatures isotopiques de l'azote permettaient d'identifier la présence d'azote d'origine anthropique dans les eaux souterraines et les eaux de surface (Kreitler 1979; Cabana et Rasmussen 1996; McClelland et al. 1997; Mayer et al. 2002). Par exemple, certains chercheurs ont établi une corrélation entre l'augmentation du pourcentage du bassin versant voué à l'agriculture et l'élévation du $\delta^{15}N$ des consommateurs aquatiques (Hebert et Wassenaar 2001; Udy et Bunn 2001; Anderson et Cabana 2005). D'autres études ont également observé un accroissement du $\delta^{15}N$ des consommateurs aquatiques avec l'augmentation de la densité de population humaine dans le bassin versant (Cabana et Rasmussen 1996; Lake et al. 2001).

De façon plus précise, certaines études ont établit une corrélation significative entre l'élévation du $\delta^{15}N$ de l'azote inorganique et des organismes aquatiques et l'accroissement des charges d'azote (quantité d'azote par unité de territoire) générées par les activités humaines pratiquées dans le bassin versant (McClelland et al. 1997; Mayer et al. 2002; Cole et al. 2004). Cela signifierait que le $\delta^{15}N$ des organismes aquatiques pourrait être utilisé comme indicateur de la quantité d'azote anthropique produite dans le bassin qui se retrouve en milieu aquatique. Le $\delta^{15}N$ des organismes aquatiques pourrait aussi potentiellement permettre d'identifier l'origine (les sources) de l'azote qui se retrouve en milieu aquatique. Les différentes sources anthropiques d'azote présentent effectivement des valeurs de $\delta^{15}N$ différentes. Par exemple, le $\delta^{15}N$ des fertilisants chimiques est faible (~0‰; Heaton 1986; Kendall 1998), tandis que celui des nitrates associées au fumier animal et aux eaux usées urbaines tend à être un peu plus élevé (+5‰ pour les excréments frais; Heaton 1986; Kendall 1998). Or, l'utilisation de ces valeurs initiales afin de distinguer les sources d'azote en milieu aquatique pourrait s'avérer problématique. En effet, l'azote provenant des fertilisants chimiques et des excrétions animales et humaines subit des transformations (une fois que les fertilisants et fumiers sont épandus dans les champs ou pendant la période de

transition des eaux usées dans les réseaux d'égouts) telles que la volatilisation et la dénitrification. Ces transformations mènent à une perte gazeuse préférentielle des isotopes légers de l'azote (^{14}N) vers l'atmosphère, résultant en une augmentation du $\delta^{15}N$ de la matière résiduelle qui demeure au sol et qui est exportée vers les milieux aquatiques (Kreitler 1979; Heaton 1986; Kendall 1998). Dans un tel cas, les diverses sources anthropiques d'azote acquièrent toutes un $\delta^{15}N$ élevé. Il pourrait conséquemment s'avérer impossible de les distinguer.

Le but du chapitre 1 est d'examiner les relations entre le $\delta^{15}N$ des consommateurs aquatiques et les charges de différentes sources d'azote liées aux activités anthropiques pratiquées dans le bassin versant. Plus spécifiquement, on y examine l'effet des charges en azote provenant des fertilisants chimiques, du fumier animal et de la population humaine sur le $\delta^{15}N$ des consommateurs primaires, des invertébrés prédateurs et des poissons. En outre, ce chapitre dresse un portrait de la variabilité spatiale du $\delta^{15}N$ pour le territoire à l'étude et permet de valider l'utilisation du $\delta^{15}N$ des consommateurs aquatiques comme indicateur des perturbations du cycle de l'azote par les activités humaines.

Objectifs spécifiques du chapitre 1 :

1. Examiner la relation entre le $\delta^{15}N$ des organismes aquatiques (invertébrés et poissons se nourrissant d'invertébrés) et les charges provenant de diverses sources d'azote liées aux activités humaines pratiquées dans le bassin versant.
2. En particulier, mesurer l'effet des charges d'azote (kg N km^{-2} an^{-1}) provenant du fumier animal, des fertilisants synthétiques, de la population humaine (excréments), ainsi que le total de ces trois charges, sur la variabilité du $\delta^{15}N$ des organismes aquatiques.

3. Mesurer la contribution relative (en pourcentage du total des charges d'azote) des trois sources d'azote énumérées ci-haut sur la variation du $\delta^{15}N$ des consommateurs aquatiques.

Ce chapitre est écrit en anglais sous forme d'article et il paraît dans la revue scientifique intitulée *Science of the Total Environment* (Volume 367, pages 968 à 978). Il est co-écrit avec le professeur Gilbert Cabana.

Chapitre 2 : Estimation de la position trophique des consommateurs aquatiques des eaux courantes à l'aide des isotopes stables de l'azote

À cause de la forte variabilité spatiale du $\delta^{15}N$ (Chapitre 1), l'estimation de la position trophique d'un consommateur à l'aide des isotopes d'azote ne peut se faire à partir de son $\delta^{15}N$ brut. Il faut plutôt corriger le $\delta^{15}N$ de ce consommateur par le $\delta^{15}N$ d'un organisme situé à la base de la chaîne alimentaire (organisme de référence). Or, ce n'est pas le $\delta^{15}N$ de n'importe quel organisme qui peut être employé comme $\delta^{15}N$ de référence. En effet, on retrouve dans les milieux lotiques divers groupes de consommateurs primaires qui présentent des comportements alimentaires variables. À titre d'exemple, on y retrouve des déchiqueteurs, qui se nourrissent de détritus d'origine terrestre, des brouteurs, qui se nourrissent d'algues, ainsi que des collecteurs, qui se nourrissent de particules diverses en suspension, dont des algues, des détritus et des petits animaux (Cummins et Klug 1979; Vannote et al. 1980). Ces différentes sources de nourriture peuvent présenter des $\delta^{15}N$ variables, ce qui influence le $\delta^{15}N$ des organismes qui s'en nourrissent. Ainsi, les divers consommateurs primaires retrouvés en milieu lotique peuvent présenter des $\delta^{15}N$ divergents. L'emploi de consommateurs primaires appartenant à des groupes fonctionnels différents entre divers sites d'étude pourrait donc générer des biais dans

le calcul des positions trophiques. Par exemple, dans une étude antérieure, nous avions observé que les collecteurs présentaient un $\delta^{15}N$ plus élevé que les autres herbivores (Anderson et Cabana 2005), suggérant un niveau trophique légèrement plus élevé. Conséquemment, l'emploi de collecteurs comme organismes de référence dans un site donné, mais de brouteurs ou de déchiqueteurs dans un second site, mènerait à un biais dans le calcul des positions trophiques et des comparaisons qui en découleraient. Dans ce cas, la variabilité inter-site de la position trophique pourrait être davantage attribuable à l'utilisation de consommateurs ayant un comportement alimentaire différent qu'à un réel changement dans la structure du réseau trophique. En somme, il importe d'uniformiser le type d'organisme de référence employé dans le calcul des chaînes alimentaires.

Certaines études isotopiques réalisées en milieu lacustre ont utilisé un nombre restreint d'organismes (moules Unionidae en particulier) en tant qu'organisme de référence afin de calculer les positions trophiques des consommateurs (Cabana et Rasmussen 1994; Cabana et Rasmussen 1996; Vander Zanden et al. 1997). Aussi, Post (2002) a analysé les différences dans le $\delta^{15}N$ de divers groupes de consommateurs en milieu lacustre et a conclu que les moules et/ou les escargots pouvaient servir d'organisme de référence dans le calcul des positions trophiques. Cependant, aucune étude de ce genre n'a été réalisée en milieu lotique à notre connaissance. Pour les fins de cette étude, il s'avérait donc nécessaire 1) d'analyser la variabilité du $\delta^{15}N$ entre les organismes de référence potentiels (consommateurs primaires) en milieu lotique et 2) sélectionner un ou quelques groupes d'organismes démontrant un $\delta^{15}N$ faible comparativement aux autres consommateurs primaires en tant qu'organismes de référence en rivière.

Le second volet du chapitre 2 consiste à estimer les positions trophiques de plusieurs organismes lotiques (invertébrés et poissons se nourrissants d'invertébrés)

en employant la méthode développée dans le premier volet. Une meilleure connaissance de la position trophique des invertébrés et des poissons qui composent une communauté permet notamment de mieux comprendre l'effet de divers processus tels que les cascades trophiques ascendantes et descendantes sur l'état global des communautés. Premièrement, la position trophique des organismes situés vers la base d'une chaîne alimentaire peut jouer un rôle important sur l'accumulation des contaminants chez les organismes situés au sommet de cette même chaîne. Par exemple, la présence de *Mysis relicta* (une espèce de zooplancton) et de certains poissons fourragers – deux types d'organismes carnivores – dans des lacs du Bouclier canadien a été associée à une plus haute position trophique du touladi (*Salvelinus namaycush*, soit le poisson au sommet de la chaîne alimentaire) capturé dans ces mêmes lacs. L'allongement de la chaîne alimentaire par l'apparition de consommateurs intermédiaires dans ces lacs a eu comme effet d'accroître les concentrations de contaminants dans les touladis via la bioamplification (Rasmussen et al. 1990; Cabana et al. 1994; Vander Zanden et Rasmussen 1996). Si ces nouveaux consommateurs avaient été des herbivores, l'effet sur l'accumulation de contaminants dans les touladis n'aurait pas été le même. La position trophique des organismes retrouvés dans une communauté modifie également l'abondance des organismes situés vers la base de cette communauté (cascades trophiques descendantes). Ainsi, plusieurs études ont observé un impact significatif de la présence ou de l'absence d'invertébrés prédateurs ou de poissons se nourrissant d'invertébrés sur la densité des algues (Power et al. 1985; Power 1992; Wooton et Power 1996). Dans ces cas, les prédateurs réduisaient de façon plus ou moins intense la densité des brouteurs, ce qui diminuait de façon plus ou moins prononcée le broutage des algues, affectant la densité d'algues. En somme, la variabilité de la position trophique des organismes situés à des niveaux intermédiaires de la chaîne alimentaire, tels que ceux examinés dans la présente étude, mérite une attention particulière. Celle-ci peut effectivement avoir des répercussions importantes sur les flux d'énergie et de contaminants vers le

sommet de la chaîne alimentaire, mais également sur la régulation des niveaux trophiques inférieurs.

Finalement, plusieurs études suggèrent que l'omnivorie (fait de se nourrir à différents niveaux dans la chaîne alimentaire) est omniprésente en milieu aquatique (Sprules et Bowerman 1988; Polis 1991). En particulier, des études examinant le comportement alimentaire de certains groupes taxonomiques d'invertébrés ont observé qu'un même groupe pouvait se nourrir de différentes ressources alimentaires (algues versus détritus, par exemple), ainsi qu'à différents niveaux trophiques (Anderson 1976; Plague et al. 1998; Zah et al. 2001). Toutefois, peu d'études ont examiné de façon simultanée la variabilité de la position trophique de plusieurs espèces d'organismes en milieu lotique, notamment parce que les mesures traditionnelles de la position trophique s'avéraient exhaustives et longues (analyses de contenus stomacaux, par exemple). Les isotopes stables d'azote semblent être un outil utile permettant de dresser un portrait rapide et réaliste de la position trophique des organismes lotiques. La seconde partie du chapitre 2 porte donc sur l'estimation de la position trophique d'un grand nombre de groupes d'invertébrés et de poissons habitant en rivière, ainsi que sur l'examen de la variabilité (omnivorie) dans ces positions trophiques.

En somme, le chapitre 2 vise, en premier lieu, à examiner et proposer une méthode permettant d'identifier un ou des organismes de référence afin d'estimer la position trophique des consommateurs lotiques à l'aide des isotopes d'azote. Plus spécifiquement, il s'agit d'examiner la variation du $\delta^{15}N$ entre les groupes fonctionnels et taxonomiques de consommateurs primaires potentiels, puis de déterminer les organismes ayant les plus faibles valeurs de $\delta^{15}N$, mais aussi une bonne répartition spatiale, comme organismes de référence. En second lieu, la position trophique de divers organismes aquatiques est estimée en employant le $\delta^{15}N$

des organismes de référence choisis selon la méthode développée. Finalement, la position trophique des invertébrés prédateurs et des poissons estimée à l'aide de la méthode développée ci-haut est comparée à la position trophique estimée à partir de la moyenne du $\delta^{15}N$ de tous les consommateurs primaires pour chaque site (pas de sélection d'organismes de référence en particulier). Cette dernière étape vise à relever la présence de biais entre ces deux méthodes.

Objectifs spécifiques du chapitre 2 :

1) Établir une méthode permettant d'identifier un ou quelques groupes d'organismes de référence quant au $\delta^{15}N$ en milieu lotique.

2) Estimer la position trophique d'organismes lotiques récoltés dans 87 sites situés en rivière en employant cette méthode (en utilisant le $\delta^{15}N$ d'un ou de quelques groupes restreints d'organismes de référence).

3) Comparer ces observations avec les positions trophiques retrouvées dans la littérature traditionnelle.

4) Examiner la variabilité des positions trophiques à l'intérieur des divers groupes taxonomiques et fonctionnels d'invertébrés et de poissons récoltés.

5) Comparer les positions trophiques des invertébrés prédateurs et des poissons mesurées à l'aide de la méthode développée (en sélectionnant une quantité restreinte de types de consommateurs primaires) avec les positions trophiques mesurées à partir d'un $\delta^{15}N$ de référence basé sur le $\delta^{15}N$ de tous les consommateurs primaires confondus.

Ce chapitre est présenté en anglais sous forme d'article co-écrit avec le professeur Gilbert Cabana. Il est publié dans le *Journal of the North American Benthological Society* (Volume 26(2), pages 273 à 285).

Chapitre 3 : Prédire la densité des communautés lotiques à l'aide de la productivité du milieu et de la position trophique

La densité des organismes est un attribut des communautés auquel se sont intéressés maints écologistes. D'ailleurs, de nombreuses études ont tenté d'élucider les facteurs qui régissent l'abondance des organismes dans la nature (Andrewartha et Birch 1961; Elton 1971; Damuth 1981). Parmi les variables examinées, la taille s'est avérée être un facteur ayant un effet déterminant sur les changements dans la densité (ou abondance) des organismes. Ainsi, plusieurs études, tant en milieu aquatique que terrestre, ont observé une diminution significative de la densité des organismes avec l'accroissement de leur taille (Damuth 1981; Peters et Wassenberg 1983; Cyr et al. 1997a; Cohen et al. 2003; Brown et al. 2004). Toutefois, une forte variabilité dans la densité des organismes à l'intérieur des diverses classes de taille examinées a été observée dans plusieurs de ces études, suggérant que d'autres variables que la taille influencent la densité des organismes.

Parmi les facteurs pouvant influencer la densité des organismes, on retrouve premièrement des facteurs ascendants (processus « bottom up ») tels que la productivité du système (énergie disponible à la base du système) et la position trophique des organismes (liée à la dissipation de l'énergie dans la chaîne alimentaire). La prédation est un second type de facteur, lié à des processus descendants (« top-down »), qui pourrait aussi affecter la densité des organismes. Finalement, la pollution anthropique pourrait aussi influencer la densité des organismes, en diminuant la densité d'organismes intolérants, mais en augmentant celle des organismes tolérants (Ford 1989). Dans le cadre du chapitre 3, trois facteurs liés à des processus ascendants seront examinés : la productivité, la température et la position trophique.

En premier lieu, le chapitre 3 examinera l'effet de la productivité sur la longueur des chaînes aquatiques. Une plus grande productivité à la base de la chaîne devrait favoriser de plus grandes densités d'organismes, puisqu'une plus grande productivité pourvoit généralement de plus grandes quantités de ressources pour l'ensemble de la communauté (plus de nourriture disponible). Un système plus productif devrait donc être en mesure de supporter de plus grandes populations de consommateurs primaires, secondaires, etc. L'accroissement de la productivité peut être favorisé par la présence de nutriments limitants la croissance des végétaux, tels que l'azote et le phosphore. D'ailleurs, plusieurs études ont observé de plus grandes densités d'organismes aquatiques dans des systèmes productifs que dans des systèmes peu productifs (Hart et Robinson 1990; Sardá et al. 1996; Perrin et Richardson 1997). Conséquemment, les activités humaines génératrices de nutriments pratiquées au sein des bassins versants (agriculture et rejets urbains; Chambers et al. 2001) pourraient induire de plus grandes densités d'organismes aquatiques. Un second facteur pouvant affecter la densité des communautés aquatiques est la température. L'activité biologique et la croissance des organismes augmentent effectivement avec la température (Cossins et Bowler 1987; Gillooly et al. 2001; Brown et al. 2004). Des températures plus élevées pourraient donc, d'une part, augmenter la production primaire algale et bactérienne (Cummins et Klug 1979; Sweeney 1984), fournissant ainsi plus d'énergie pour des consommateurs supérieurs. D'autre part, elles pourraient aussi accélérer la croissance des invertébrés et ainsi favoriser le maintien de plus grandes densités d'organismes.

Ces deux facteurs peuvent influencer différemment les densités des diverses classes de taille présentes dans une communauté. Par exemple, Cyr et al. (1997b) ont observé que la densité des petits organismes augmentait de façon plus rapide que la densité des gros organismes en fonction d'un accroissement dans la productivité. Par conséquent, on pourrait s'attendre non seulement à observer de plus grandes densités d'organismes en milieu productif, mais aussi d'observer une augmentation plus

prononcée de la densité des petits organismes par rapport aux plus gros. La température pourrait aussi affecter différemment la densité des diverses classes de taille. Premièrement, de plus chaudes températures pourraient favoriser une augmentation plus importante de la densité des petits organismes, ces derniers ayant un taux de croissance généralement plus rapide que les gros organismes (Hennemann 1983; Gillooly et al. 2001; Savage et al. 2004). À l'inverse, considérant que les températures plus élevées accélèrent la croissance des organismes, on pourrait s'attendre à retrouver de plus grandes densités de gros organismes, plus matures, dans les sites plus chauds (Sweeney 1984; Hellawell 1986).

La position trophique est un troisième facteur qui pourrait influencer la densité des organismes aquatiques et qui sera examiné dans le chapitre 3. Suivant la théorie sur l'efficacité de transfert énergétique, les prédateurs devraient être moins abondants que les herbivores de même taille parce que l'efficacité de transfert de l'énergie entre les niveaux trophiques diminue à mesure que l'on s'élève dans la chaîne alimentaire (Lindeman 1942; Slobodkin 1963; Kerr et Dickie 2001). Ainsi, un organisme occupant une position trophique élevée aura plus de difficulté à tirer de l'énergie du système qu'un organisme plus bas dans la chaîne alimentaire, cette dernière s'étant dissipée via les niveaux trophiques inférieurs (respiration, excrétions, etc.). Conséquemment, une plus grande proportion de prédateurs dans une classe de taille donnée devrait être associée à une plus faible densité d'organismes dans cette même classe.

Les positions trophiques des classes de taille seront estimées à l'aide des isotopes stables d'azote, selon la méthode déjà établie dans le chapitre 2. L'utilisation des isotopes stables d'azote dans la mesure des positions trophiques permet, d'une part, de mesurer rapidement la position trophique moyenne des classes de taille sans avoir recours à des méthodes qui sous-estiment l'omnivorie ou qui demandent un effort d'échantillonnage ou d'identification exhaustifs. D'autre part, l'utilisation de la

position trophique de la classe de taille complète, sans identifier et caractériser chacun des organismes qui la composent (méthode ataxonomique, où l'on estime la position trophique de toute la biomasse caractérisant une classe de taille), permet de dresser un portrait d'ensemble des interactions trophiques dans la communauté (flux d'énergie).

En somme, le but du chapitre 3 est de tenter de prédire la densité des communautés d'organismes aquatiques (entières ou par classes de taille) à l'aide de trois variables liées à des processus ascendants : la productivité, la température et la position trophique. Le chapitre 3 permet, d'une part, d'examiner comment la densité répond à différents facteurs environnementaux et, d'autre part, comment les isotopes stables d'azote peuvent être employés comme mesure de la structure des communautés (en ce qui concerne la densité).

Objectifs spécifiques du chapitre 3 :

1) Examiner la variation dans la densité des communautés lotiques et dans la position trophique en fonction de la taille et ce, en utilisant une méthode ataxonomique (moyenne de la densité et de la position trophique pour tous les organismes amalgamés par classe de taille).

2) Examiner la variation dans la densité de chaque classe de taille en fonction de la productivité du milieu (azote, phosphore, chlorophylle *a*) et de la température.

3) Examiner les changements dans la densité de chaque classe de taille en fonction de la position trophique moyenne de ces classes (mesurée à l'aide du $\delta^{15}N$).

4) Examiner l'effet combiné de la taille, de la productivité (azote, phosphore, chlorophylle *a*), de la température et de la position trophique sur la variation dans la densité pour la totalité de la communauté aquatique (tous les sites et toutes les classes de taille inclus).

Ce chapitre est présenté en anglais sous forme d'article. Il a été co-écrit avec le professeur Gilbert Cabana. Il sera soumis prochainement.

Chapitre 4 : Altération de la structure des réseaux trophiques lotiques par les activités humaines: une approche isotopique

Plusieurs études antérieures ont proposé que la productivité, ainsi que le niveau de perturbation d'un milieu peuvent altérer la longueur des chaînes alimentaires dans la nature (Fretwell 1977; Oksanen 1981; Odum 1985; Menge et Sutherland 1987). En particulier, ces études théoriques suggèrent que les milieux productifs devraient supporter un plus grand nombre de niveaux trophiques (plus d'énergie à la base de la chaîne alimentaire) que les milieux peu productifs, générant ainsi de plus longues chaînes. À l'inverse, les perturbations provoqueraient une élimination des espèces intolérantes, ce qui générerait de courtes chaînes dans les sites perturbés. Plusieurs études empiriques appuient ces théories et ont observé des chaînes alimentaires plus longues dans les milieux productifs (Jenkins et al. 1992; Townsend et al. 1998; Thompson et Townsend 2005), mais simplifiées (plus courtes) dans les milieux perturbés (Jenkins et al. 1992; Sherwood et al. 2002). Puisque les activités humaines pratiquées au sein d'un bassin versant sont à la fois une source de productivité et de perturbation, ces dernières devraient avoir un impact sur la structure des communautés aquatiques. En particulier, les chaînes alimentaires devraient être plus longues dans les sites productifs (agricoles ou urbains), où les rejets en azote et en phosphore sont plus importants, mais plus courtes dans les milieux affectés par des rejets d'origine industrielle, les contaminants industriels étant considérés comme une perturbation.

Tel que mentionné précédemment, la plupart des études antérieures qui ont examiné l'effet de la productivité et des perturbations sur les communautés

aquatiques présentaient diverses lacunes quant aux façons de mesurer la longueur des chaînes. Dans ce chapitre, nous proposons d'utiliser les isotopes stables d'azote en tant qu'indicateurs rapides et réalistes de la structure des communautés. En somme, l'objectif premier du chapitre 4 est donc d'examiner l'utilité des isotopes stables d'azote en tant qu'indicateur de la structure des communautés habitant dans des rivières affectées par différents types d'activités anthropiques. En particulier, deux mesures de la longueur de chaîne basée sur les isotopes stables de l'azote seront employées : la position trophique des poissons se nourrissant d'invertébrés et la relation δ^{15}N-taille de la communauté d'invertébrés. Ces deux mesures donnent des informations différentes et complémentaires sur le réseau trophique. La position trophique des poissons devrait être un intégrateur de la structure de la communauté d'invertébrés, les poissons se nourrissant à partir de cette dernière. Par exemple, la présence d'invertébrés prédateurs dans la communauté devrait augmenter la position trophique des poissons qui s'en nourrissent. Pour ce qui est de la relation δ^{15}N-taille, elle repose sur l'examen des valeurs moyennes de δ^{15}N de toute la biomasse d'invertébrés dans la communauté combinée par classe de taille. Tel que mentionné plus tôt, cette approche est ataxonomique (moyenne de la position trophique par classe de taille, sans égard aux taxons présents; voir chapitre 3) et elle permet de dépeindre les grandes interactions trophiques caractéristiques de la communauté. En effet, plus il y a de prédateurs dans une classe de taille donnée, plus le δ^{15}N de cette classe devrait être élevé. Aussi, plus la proportion de prédateurs augmente avec la taille, plus la pente δ^{15}N-taille devrait être élevée. Finalement, dans le cadre du présent chapitre, il sera question d'examiner les relations entre ces deux mesures basées sur les isotopes stables de l'azote et reflétant la longueur de la chaîne alimentaire et 1) les concentrations de chlorophylle *a* dans l'eau (indicateur de la productivité) et 2) le nombre d'industries avec un potentiel de rejet de polluants vers les milieux aquatiques dans le bassin versant (indicateur de perturbation). Il s'agira aussi d'examiner comment ces deux mesures répondent à la présence de prédateurs

dans la communauté d'invertébrés. Cette seconde analyse permettra de déterminer si les mesures isotopiques employées reflètent bel et bien certaines caractéristiques trophiques de la communauté.

Objectifs spécifiques du chapitre 4 :

1) Examiner la variabilité de la position trophique et des pentes δ^{15}N-taille entre les sites d'étude.

2) Déterminer si la position trophique et les pentes δ^{15}N-taille sont influencées par la productivité (chlorophylle *a* dans l'eau) et les perturbations (nombre d'industries avec un potentiel de rejet de polluants dans le bassin versant).

3) Examiner l'effet des prédateurs sur la variabilité de la position trophique et des pentes δ^{15}N-taille.

4) En somme, déterminer si la position trophique et la pente δ^{15}N-taille peuvent être employées comme indicateurs de la structure des communautés dans des rivières touchées par différents types de perturbations anthropiques.

Ce chapitre est présenté en anglais sous forme d'article. Il a été co-écrit avec le professeur Gilbert Cabana. Il sera soumis prochainement.

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CHAPITRE 1

LE $\delta^{15}N$ DES RÉSEAUX TROPHIQUES LOTIQUES REFLÈTE-T-IL LA QUANTITÉ ET L'ORIGINE DES CHARGES D'AZOTE PROVENANT DU BASSIN VERSANT?

DOES $\delta^{15}N$ IN RIVER FOOD WEBS REFLECT THE INTENSITY AND ORIGIN OF N LOADS FROM THE WATERSHED?

Résumé

Les signatures isotopiques de l'azote ($\delta^{15}N$) d'invertébrés et de poissons collectés dans 82 sites localisés dans des rivières des plaines du Saint-Laurent au Québec, Canada, ont été mesurées afin d'examiner la relation entre le $\delta^{15}N$ des consommateurs aquatiques et les charges en azote (N) d'origine anthropique dans le bassin versant. Les valeurs moyennes de $\delta^{15}N$ mesurées chez les trois niveaux trophiques examinés (consommateurs primaires, invertébrés prédateurs et poissons se nourrissant d'invertébrés) étaient fortement corrélées aux charges totales d'azote anthropique sur le bassin versant (kg N km^{-2} an^{-1}; $r^2 > 0.61$, $p < 0.0001$), ainsi qu'aux charges d'azote provenant du fumier animal ($r^2 > 0.62$, $p < 0.0001$), des fertilisants chimiques ($r^2 > 0.45$, $p < 0.0001$) et de la population humaine ($r^2 > 0.29$, $p < 0.0001$). Des relations significatives ont également été observées entre le $\delta^{15}N$ des consommateurs primaires et les charges d'azote provenant de trois types de bétail (bovins, porcs et volaille; $p < 0.0001$). De plus, ces trois espèces animales contribuaient de façon significative et indépendante à l'élévation du $\delta^{15}N$ des consommateurs primaires (r^2 multiple = 0.67, $p < 0.0001$). Des régressions curvilinéaires ont été observées à tous les niveaux d'analyse, les valeurs de $\delta^{15}N$ augmentant lentement lorsque les charges d'azote étaient faibles, mais de façon beaucoup plus prononcée au fur et à mesure que ces charges augmentaient. Les trois sources d'azote anthropiques examinées étaient fortement corrélées les unes avec les autres, ce qui nous a empêché d'isoler leur effet respectif sur la variation du $\delta^{15}N$. Lorsque ces charges furent exprimées en pourcentage du total des charges en azote, le $\delta^{15}N$ des consommateurs aquatiques demeura fortement corrélé avec les charges provenant du fumier et des fertilisants, mais pas avec les charges d'azote provenant de la population humaine. En somme, ces résultats suggèrent que le $\delta^{15}N$ des consommateurs aquatiques peut être utilisé comme indicateur de l'intensité des charges en azote anthropique sur le bassin versant. Cependant, il ne s'avère pas un traceur efficace des sources individuelles et distinctes d'azote.

Abstract

Stable nitrogen isotope ratios ($\delta^{15}N$) were measured in invertebrates and fish collected from 82 river sites located in the Saint-Lawrence Lowlands in Québec, Canada, to examine the relationship between aquatic biota $\delta^{15}N$ and anthropogenic nitrogen (N) loads. Mean $\delta^{15}N$ values of all three trophic levels examined (primary consumers, predatory invertebrates and invertebrate-feeding fish) were highly correlated with total anthropogenic N loads on the watershed (kg N km^{-2} yr^{-1}; $r^2 > 0.61$, $p < 0.0001$) and with N loads originating from livestock manure ($r^2 > 0.62$, $p < 0.0001$), synthetic fertilizers ($r^2 > 0.45$, $p < 0.0001$), and human population ($r^2 > 0.29$, $p < 0.0001$), respectively. Significant relationships were also observed between primary consumer $\delta^{15}N$ and N loads originating from each of the three livestock species examined (bovines, pigs and poultry; $p < 0.0001$). Furthermore, all three animal species contributed significantly and independently in elevating primary consumer $\delta^{15}N$ (multiple $r^2 = 0.67$, $p < 0.0001$). Curvilinear regressions were observed at all levels of analysis, $\delta^{15}N$ values increasing slowly over a wide range of low levels of N loads, but increasing much faster as N loads grew larger. The three anthropogenic N sources examined were highly correlated with one another, preventing us from statistically isolating their respective effects on $\delta^{15}N$. When these loads were expressed as a proportion of total N load, $\delta^{15}N$ of aquatic biota was still highly correlated with N from livestock and fertilizers, but not with N from human population. Overall, these results suggest that $\delta^{15}N$ values of aquatic consumers could be used as indicators of the intensity of anthropogenic N loading on watersheds, but not as tracers of the relative importance of individual N sources.

Keywords: Fertilizers, Human, Isotope, Manure, Nitrogen, Watershed

1.1. Introduction

Agriculture and other human activities such as combustion of fossil fuel have altered the global nitrogen (N) cycle substantially (Vitousek et al. 1997; Tilman 1999; Galloway and Cowling 2002). In the second half of the 20th century, N inputs to terrestrial systems have practically doubled (Vitousek et al. 1997; Howarth et al. 2002), resulting in important N losses to aquatic ecosystems. N enrichment of aquatic ecosystems has lead to eutrophication and deterioration of aquatic communities (Howarth 1998; Rabalais 2002), and has been shown to be toxic to human consumption (Wolfe and Patz 2002). Anthropogenic N in rivers and lakes principally originates from agricultural activities and urban runoffs. In particular, synthetic fertilizers, livestock manure and urban wastewater are amongst the most common N sources in rivers and lakes worldwide (Vitousek et al. 1997; Howarth 1998; Green et al. 2004). Better knowledge of the respective effects of various anthropogenic N sources on aquatic ecosystems is needed to understand the consequences of future changes in N inputs, as growth in food production may necessitate and generate considerably larger amounts of nutrients (Tilman 1999).

Stable nitrogen isotope ratios ($\delta^{15}N$) measured in inorganic N fractions (e.g., NO_3 NH_4; Kreitler 1979; Mayer et al. 2002) and biota (Cabana and Rasmussen 1996; McClelland et al. 1997) have been used as indicators of anthropogenic sources in ground water and aquatic ecosystems. Different anthropogenic N sources often have different initial isotopic values, thus potentially allowing their identification from $\delta^{15}N$ values observed in inorganic N fractions, primary producers and consumers. For instance, $\delta^{15}N$ values of synthetic fertilizers have been shown to have low $\delta^{15}N$ values (~0‰; Heaton 1986; Kendall 1998), whereas nitrates derived from animal manure and wastewater tend to exhibit slightly higher initial values (freshly produced excretions: +5‰; Heaton 1986; Kendall 1998). Although some studies have used

these values to track anthropogenic sources in aquatic systems, using them to trace alternate sources of N might be misleading. Indeed, N from both synthetic fertilizers and animal manure can be transformed on the watershed by processes such as volatilization and denitrification, which lead to gaseous losses of N and elevated $\delta^{15}N$ of the remaining unreacted N. Hence, these sources generally acquire higher $\delta^{15}N$ values than their initial values (up to +14‰ for synthetically fertilized field soils, and +10 to +25‰ for animal excretions; Kreitler 1979; Heaton 1986; Kendall 1998). Such transformations might confuse the respective importance of N sources and render impossible the disentangling of these sources.

The goal of this study is to examine the relationships between $\delta^{15}N$ values of aquatic consumers and anthropogenic N sources from watersheds. In particular, we examine the effects of N loads originating from human population, livestock manure and synthetic fertilizers on $\delta^{15}N$ values of invertebrate primary consumers, predatory invertebrates and invertebrate-feeding fish. In addition, we examine how aquatic biota $\delta^{15}N$ values are associated with the relative contribution (%) of each of these sources to total inorganic N inputs (including regional atmospheric deposition). A few previous studies have investigated the impact of different anthropogenic N loads on $\delta^{15}N$ of river or coastal inorganic N fractions and biota (e.g., McClelland et al. 1997; Mayer et al. 2002), and we complement these studies with a large network of 82 river sites (a total of 1206 samples).

1.2. Materials and Methods

1.2.1. Study Sites and sampling

During the summer of 2000, invertebrates and fish were sampled from 82 river stations in 13 watersheds draining the St-Lawrence Lowlands, Québec, Canada (Fig. 1.1). Study sites were all located in riffle sections. Watersheds ranged from 32

to 42 730 km² (mean = 3214 km²) and were characterized by varying land use types. Areas devoted to agriculture in 2001 (pasture and crops) ranged from 0 to 52% (13.5% on average), while population density ranged from 0 to 127 inhabitants per square kilometer (mean = 20.6 inhabitants km^{-2}). Watersheds located on the south shore of the Saint-Lawrence River were more heavily impacted by human activities, whereas watersheds located north of the Saint-Lawrence River were generally mostly forested (Anderson and Cabana 2005).

Invertebrates (primary consumers and predators) and fish were captured with D-frame aquatic nets. Samples were kept in coolers and frozen within 8 hours and then thawed for sorting and identification. Invertebrates were identified to family or genus according to Merritt and Cummins (1996) and Thorp and Covich (1991), while fish were identified to the species, following Scott and Crossman (1974). Once identified, all samples were dried at 60°C for at least 48 hours, ground into a homogenous powder and sent for isotopic analysis at the University of New Brunswick where their isotopic composition was determined with a Finnigan-Mat Delta Plus mass spectrometer. Invertebrates were used whole and guts were not cleared or removed prior to isotopic analyses. Previous studies suggest that gut clearance has a negligible impact on overall isotopic values of organisms (Junger and Planas 1994; Jardine et al. 2005). A subset of samples was analysed in duplicates and yielded a mean standard deviation of 0.17‰ for 93 pairs. Further details on the classification and identification of consumers can be found in Anderson and Cabana (2005).

1.2.2. Watershed delineation and N load estimates

Watersheds for all 82 sites were delineated with ArcInfo 8.0.2 (ESRI Inc., Redlands, California) and TOPAZ 1.20 (Martzl and Garbrecht, developers; http://duke.usask.ca/~martzl/topaz/index.html) using topographic and hydrological

geo-referenced databases from Natural Resources Canada (National Topographic Data Base; http://www.cits.rncan.gc.ca).

N loads on watersheds were estimated for three anthropogenic sources: N excreted by human population, N excreted by livestock, and synthetic fertilizer N applied to fields. In order to estimate percent contribution of these three anthropogenic sources relative to total inorganic N inputs, we also estimated background N loads from atmospheric deposition. Throughout the text, anthropogenic N will refer to the first three sources (although part of atmospheric deposition might be of anthropogenic origin), whereas total inorganic N will refer to the sum of all four sources.

Data on human and livestock populations at the municipality level were obtained from the 2001 Canadian Census and the 2001 Canadian Agricultural Census (Statistics Canada 2002a, 2002b). N produced by livestock was estimated for each municipality by multiplying livestock numbers with the estimated N excreted yearly (kg N yr^{-1}) by species (bovines, pigs and poultry) and age classes (Table 1.1). We assumed here that livestock manure was applied in the municipality where it was produced. Previous reports indeed suggest that manure is typically applied locally and is seldom transported over long distances, generally because of high transportation costs (Johnes et al. 1996 and references therein; Ministère de l'Environnement du Québec 2003). N excreted by humans was estimated by multiplying population numbers by the mean N expected to be produced by a human for a year (4.4 kg N yr^{-1}; Meybeck 1982). Data on synthetic fertilizers were also obtained at the municipality level and corresponded to the amounts of N in fertilizers sold by municipality for the year 1995 (kg N yr^{-1}; provided by the Ministère de l'Environnement du Québec, Direction des politiques du secteur agricole). We assumed that fertilizers were applied in the municipality where they were sold. Finally, these three nitrogen sources (livestock manure, human population and

synthetic fertilizers) were summed up to yield total anthropogenic N (excluding atmospheric deposition).

To estimate how much N from these sources was produced on the 82 study watersheds, we first associated data on N amounts produced by human population, livestock species, and fertilizers at the municipality level with each municipality (represented by polygons) in MapInfo 6.5 (MapInfo Corporation, Troy, New York). Watersheds delineations were then superimposed over the municipalities polygons, and the MapInfo function 'split' was used to divide the municipalities attributes (e.g., amounts of N) in proportion to their area inside the watersheds limits. Next, information associated with portions of municipalities positioned within a watershed was summed up to yield total N amounts for each N source produced on this watershed. Finally, to estimate N loads, N amounts produced on a watershed were divided by watershed area (thus normalizing for watershed area). Note that the estimated N amounts correspond to the N inputs on the watershed upstream of each sampling site.

To calculate the contribution of these three N sources relative to total inorganic N inputs on our watersheds, we then estimated regional wet and dry N deposition. We used estimates from Janzen et al. (2003), who suggested an average deposition of 500 kg N km^{-2} yr^{-1} on Canadian landscapes not adjacent to anthropogenic emissions. This estimate takes into account N from natural sources (lightning, soils) and N released by anthropogenic activities at a broad spatial scale. It, however, does not include atmospheric deposition associated with local anthropogenic activities. Previous studies have shown that ammonia originating from livestock was transported over small distances (< 500 meters; Pitcairn et al. 1998; Fowler et al. 1998). Hence, we did not include such often high estimates of local deposition to avoid counting twice the N applied to soils (e.g., N in manure and fertilizers which was volatilized and deposited close by).

1.2.3. Statistical analysis

Mean $\delta^{15}N$ values were calculated for primary consumers, predatory invertebrates, and insectivorous fish, respectively. A previous analysis of the differences among functional feeding groups of primary consumers for the current study sites (Anderson and Cabana 2005) suggested that variability in $\delta^{15}N$ was low among these different functional feeding groups (typically < 1‰ within sites), in comparison to inter-site variability (> 13‰). Thus, all organisms characterized as primary consumers were combined to yield the mean primary consumer $\delta^{15}N$ used in this study. Relationships among the three anthropogenic N loads (human population, synthetic fertilizers and livestock manure), and relationships between $\delta^{15}N$ and percent contribution of anthropogenic N sources to total inorganic N load were examined using linear regression analyses. Since relationships between $\delta^{15}N$ and nitrogen loads could be non linear or showing thresholds, we chose to examine them using polynomial regression analyses (Zar 1999) in order to capture this potential complexity. In addition, the relative contribution of N loads from three animal species (bovines, pigs and poultry) was also analysed using a multiple regression analysis. The correlation between two of these variables was slightly over 0.70 ($r = 0.71$ between N loads originating from bovines and pigs), suggesting a slight collinearity, which could have weakened the analysis (Tabachnick and Fidell 2001). Nevertheless, we chose to proceed with a multiple regression analysis, since this collinearity was relatively small and absent from other pairs of variables. Presence of spatial autocorrelation among river sites was previously examined (see Anderson and Cabana 2005) and showed significant spatial autocorrelation for the sites on the du Loup River (4 sites; Fig. 1.1k). Thus, only the most downstream du Loup river site was used in the regression analyses, while the other three sites were removed (for a total number of 79 sites instead of 82). All analyses were performed using SYSTAT (Version 8.00, SPSS Inc.) and SAS (Version 8.0, SAS Institute Inc.). Percentages

were arcsine transformed and N loads were log-transformed prior to statistical analyses in order to meet regressions assumptions (Zar 1999).

1.3. Results

1.3.1. Nitrogen loads and sources

Total nitrogen loads attributable to human population, fertilizers and livestock (combined) on watersheds ranged from 2.5 to 6781.2 kg N km^{-2} yr^{-1} (mean = 1482.2 kg N km^{-2} yr^{-1}, s.d. = 1552.8). Among the three N sources, N loads originating from livestock manure were larger than loads originating from human population and synthetic fertilizers (Fig. 1.2). For instance, N loads attributable to livestock manure were, on average, eleven times greater than loads originating from human population (mean ratio = 11.1:1; range = 0.2:1 to 42.7:1). All three nitrogen sources were correlated with one another (Fig. 1.2), suggesting that at the regional scale, population and agricultural areas tend to develop close to one another in southern Québec.

Bovine manure constituted the principal source of animal N in our watersheds, accounting on average for 68% of total manure N loads (2 to 100%) generated on watersheds. N originating from pigs and poultry represented less important sources, with 18% coming on average from pigs, and 14% from poultry. Although pigs were more abundant on watersheds than bovines (an estimated average of 39 pigs km^{-2}, versus 12 bovines km^{-2} (all types and age classes confounded)), a single bovine typically excreted much more N than a pig (Table 1.1), generating this large difference in N loads. Similarly, poultry (263 individuals km^{-2} per watershed on average) excreted much less N than pigs and bovines and thus had a lesser influence on total N loads. All three animal sources were significantly correlated with one another among study sites ($0.50 \geq r^2 \geq 0.19$, $p < 0.0001$).

1.3.2. Relationships between aquatic consumer $\delta^{15}N$ and N loads

Mean $\delta^{15}N$ values of aquatic organisms were significantly correlated with anthropogenic nitrogen loads (human population, livestock manure, and synthetic fertilizers altogether; Fig. 1.3; Table 1.2) on watersheds upstream of sampling sites. Cubic or quadratic regressions best explained the relationships for the three indicator groups (primary consumers, predatory invertebrates and fish), showing small increases in $\delta^{15}N$ when N loads were inferior to ~300 kg N km^{-2} yr^{-1}, but more consistent increases when this threshold was exceeded. Mean primary consumer $\delta^{15}N$ was also well correlated with the amounts of N originating from livestock manure, human population and fertilizers, respectively (Fig. 1.4; Table 1.2). Mean $\delta^{15}N$ for predatory organisms (invertebrates or fish) also significantly increased with N loads for all three N sources (Table 1.2), but their correlation coefficients were generally slightly lower than for primary consumers, justifying the use of primary consumer $\delta^{15}N$ alone in subsequent analyses. Overall, the variation in $\delta^{15}N$ explained by human population N loads (r^2 = 0.29 to 0.46) was much lower than that obtained for fertilizers (r^2 = 0.45 to 0.62) and manure (r^2 = 0.62 to 0.73).

Within livestock manure sources, primary consumer $\delta^{15}N$ seemed to be more strongly correlated with N loads associated with bovines and pigs than with poultry (Fig. 1.5), although all relationships were significant. Relatively low collinearity among these three animal sources enabled us to proceed with a multiple regression analysis. All three animal species contributed significantly ($p < 0.05$) to the multiple regression equation (multiple $r^2 = 0.67$, $p < 0.0001$):

$$\delta^{15}N_{\text{primary consumer}} = 2.63 + 1.27\,[\log (N_{\text{bovine}} +1)] + 0.66\,[\log (N_{\text{pig}} +1)] + 0.58\,[\log (N_{\text{poultry}} +1)] \quad (1)$$

N_{bovine}, N_{pig} and $N_{poultry}$ corresponding respectively to the N loads (kg N km^{-2} yr^{-1}) originating from bovines, pigs and poultry species listed in Table 1.1. As shown by the regression coefficients, changes in bovine N loads tended to have a larger influence on primary consumer $\delta^{15}N$ than changes in other farm animals N loads.

1.3.3. $\delta^{15}N$ and relative contribution of N sources

Livestock manure constituted 37% of total inorganic N loads (including atmospheric deposition) on watersheds, on average (ranging from 0 to 82%). Synthetic fertilizers and human population accounted respectively for 15% (0 to 57%) and 5% (0 to 25%) of total N loads. Primary consumer $\delta^{15}N$ was significantly correlated with percent contribution of fertilizer N ($r^2 = 0.36$, $p < 0.0001$) and manure N ($r^2 = 0.55$, $p < 0.0001$) to total inorganic N load (Fig. 1.6). However, $\delta^{15}N$ values were not correlated with percent N originating from human population ($p < 0.05$).

1.4. Discussion

1.4.1. Nitrogen loads and sources

Results showed that livestock manure constituted the largest anthropogenic N source in southern Québec watersheds, excluding the Saint-Lawrence River (e.g. excluding the city of Montréal, with its 3 000 000 inhabitants). This is attributable to the fact that livestock numbers were, on average, greater than human population (pigs and bovines numbers altogether were twice as high as human population numbers), and that bovines and pigs excreted much more N than a human (e.g., ratio of 19:1 between a dairy cow and a human; Table 1.1). Similarly, bovines contributed more to total N loads than other farm animals, since they produced larger amounts of N per capita per year. N inputs originating from bovines, pigs, and poultry were generally not highly correlated with one another, which can be attributable to their different

raising requirements. For instance, pigs tend to be raised indoors, in industrial barns, while bovines are often raised outdoors on pasture fields.

When compared to other countries and continents, anthropogenic N loads measured in the present study tend to be moderate. For instance, Howarth et al. (1996) have shown that the Saint-Lawrence basin (including this study's sites) received lower N loads than most watersheds of the North Atlantic Ocean during the 1980's. They reported that, on average, the Saint-Lawrence basin received 1168 kg N km^{-2} yr^{-1}, a loading consistent with our mean of 1436 kg N km^{-2} yr^{-1}. In comparison, watersheds of western Europe and of the eastern United States of America were characterized by total N loads ranging from 2200 to 7044 kg N km^{-2} yr^{-1}. Moreover, in terms of population density, our watersheds (mean of 20.6 people km^{-2}) were well below the average of west European watersheds (47 to 186 inhabitants km^{-2}), eastern North American watersheds (> 31 inhabitants km^{-2}; except the Mississippi River watershed at 20 inhabitants km^{-2}; Howarth et al. 1996), and other large world rivers such as the Ganges (> 300 inhabitants per km^2 in the early 1990's; Peierls et al. 1991). As for fertilizer applications, mean loads in the present study (409 kg N km^{-2} yr^{-1}) were also smaller than the European or American loads estimated during the 1980's (600 to 5960 kg N km^{-2} yr^{-1} Howarth et al. 1996). According to Green et al. (2004), contemporary N loads attributable to fertilizers in North America (including this study's watersheds) were also much smaller (~four times smaller) than loads on Asian watersheds, but higher than those found in Africa and Australia. Furthermore, in the case of livestock N, North American loads were lower than most continents (Green et al. 2004). Overall, these values suggest that the N loads measured in the present study are conservative compared to those observed in other parts of the world.

1.4.2. Relationships between aquatic consumer $\delta^{15}N$ and N loads

Mean $\delta^{15}N$ values of aquatic consumers (all three trophic levels) were well correlated with anthropogenic N loads on watersheds. Increases in $\delta^{15}N$ with N loads originating from livestock manure, synthetic fertilizers and human population can be attributable to different processes. First, N originating from humans and animals tend to show slightly higher initial $\delta^{15}N$ values than fertilizers (+5‰ in animals versus ~0‰ for fertilizers, respectively; Kendall 1998). However, these values are not high enough to account for all of the variability in $\delta^{15}N$ among our study sites (e.g., +1.8‰ to +15.1‰ for primary consumers). Rather, N transformations such as volatilization and denitrification that occur after N has been applied to fields or when it is transported through sewage systems could be the principal factor leading to these high $\delta^{15}N$ values. For example, Heaton (1986) and Kendall (1998) have noted elevated $\delta^{15}N$ values for manure and human dejections which had been subject to such N transformations. Similarly, Kreitler (1979) has observed high $\delta^{15}N$ values (up to 14‰) in environments affected by runoffs of synthetic fertilizer N, an observation also supported by Högberg (1990) who found important increases in $\delta^{15}N$ of systems saturated with fertilizers, despite their low initial $\delta^{15}N$ value. In the present study, continuous increases in $\delta^{15}N$ in watersheds where amounts of synthetic fertilizers applied were large (Fig. 1.4) tend to suggest that N from fertilizers also acquires high $\delta^{15}N$ values while transported to aquatic systems, as does livestock manure and human population N. Hence, transformation of N sources before they enter streams and rivers is likely responsible for the high $\delta^{15}N$ values measured in the present study's food webs. However, other N transformations could have counteracted this effect. For example, fractionation associated with nitrification of ammonium can generate light $\delta^{15}N$ nitrates (Högberg 1997), which, if directly assimilated, can be passed up the food chain and result in aquatic consumers having lower $\delta^{15}N$. Nevertheless, elevated $\delta^{15}N$ values of biota collected in agricultural sites suggest that

N-transformations accompanied by N losses from the system (denitrification, volatilization) are overriding such potential effects. Additionally, in-stream transformations could also have affected the $\delta^{15}N$ values measured (Kellman and Hillaire-Marcel 1998; Kendall 1998; Battaglin et al. 2001), and future work might help to better understand the importance of such processes on aquatic biota $\delta^{15}N$.

Our study suggests that loads from all three anthropogenic sources potentially contributed to elevation in $\delta^{15}N$ values of aquatic consumers. However, high collinearity among the three N sources made it difficult to ascertain the independent contribution of each source to elevated aquatic consumer $\delta^{15}N$. McClelland et al. (1997) and Cole et al. (2003) have reported that the use of percent contribution of N sources to total N load could help distinguish the relative influences of different N sources on aquatic biota $\delta^{15}N$. Using this approach, we found that only manure and fertilizers contributed in elevating aquatic consumer $\delta^{15}N$. In general, percent contribution of livestock manure N was more strongly correlated with primary consumer $\delta^{15}N$ than the other anthropogenic sources. Moreover, livestock manure N loads were also more strongly correlated with aquatic consumer $\delta^{15}N$. These results suggest that livestock manure N loads potentially had a greater influence on aquatic consumer $\delta^{15}N$ than did the two other anthropogenic N sources.

Previous studies have shown how livestock numbers on watersheds contributed to important losses of nutrients into aquatic ecosystems (Johnes et al. 1996; Carpenter et al. 1998; Berka et al. 2001). Typically, manure is applied in great quantities to fields to promote the growth of crops. However, with continuous applications of excess nutrients, the storage and assimilation capacity of soils and plants is rapidly exceeded and nutrients originating from manure find their way to rivers and lakes. Our study shows that N originating from anthropogenic activities not only leaches to aquatic systems, but is also incorporated into entire aquatic food

webs. This is supported by the fact that all aquatic consumers collected in impacted sites exhibited high $\delta^{15}N$ values. Likewise, other studies using nitrogen isotopes as tracers of anthropogenic N sources have shown how wastewater and manure N discharges generated increases in $\delta^{15}N$ of aquatic biota and inorganic N fractions (McClelland et al. 1997; McClelland and Valiela 1998; Mayer et al. 2002). In particular, McClelland et al. (1997) and Cole et al. (2003) have reported that wastewater N loads significantly increased primary producer $\delta^{15}N$. We did not observe significant correlations between primary consumer $\delta^{15}N$ and human population N. This apparent discrepancy could be attributed to differences in the techniques used to estimate N loads. For instance, we have used direct inputs of N on watersheds to estimate N loads, whereas McClelland et al. (1997) and Cole et al. (2003) have estimated N loads reaching estuaries after accounting for N losses and retention. Moreover, the watersheds studied by McClelland et al. (1997) were dominated by urban areas (Cape Cod region), whereas our study watersheds were dominated by agriculture, with more modest N inputs from human population. Hence, predominance of livestock manure in our watersheds might have masked the effects of other sources such as human population and fertilizer N.

In contrast with livestock manure, $\delta^{15}N$ values of aquatic consumers (all three trophic levels) were weakly correlated with N loads originating from human population. This weaker relationship was associated with the presence of sites showing high population N loads but very low $\delta^{15}N$ values (Fig. 1.4a). Three of these sites were further investigated and results revealed that they were all affected, at the time of sampling, by large untreated domestic and/or industrial point-source discharges. Further analysis of the particulate organic matter (POM) of the affluent (before treatment) and the effluent (after treatment) of the sewage treatment plants located closely upstream of two of these sites showed that the untreated POM exhibited low $\delta^{15}N$ values (affluent: range = -0.13 to +1.15‰, mean = +0.35‰, s.d. =

0.57‰) in comparison with the treated POM (effluent: range: +2.21 to +8.18‰, mean = +5.16‰, s.d. = 3.29‰). Hence, occasional untreated sewage overflows (as reported by these facilities) with low $\delta^{15}N$ might be responsible for the weaker relationships observed between $\delta^{15}N$ and population N. Previous studies have observed similar decreases in aquatic biota $\delta^{15}N$ in aquatic systems affected by untreated sewage discharges (Rau et al. 1981; Van Dover et al. 1992; Tucker et al. 1999). In addition, a study conducted by deBruyn and Rasmussen (2002) showed how such low $\delta^{15}N$ POM originating from a sewage treatment plant got incorporated in aquatic food webs downstream of the effluent. Our findings agree with this observation, since low $\delta^{15}N$ values were observed for all three trophic levels collected at these impacted sites.

Within the livestock manure source, bovines, pigs and poultry were all found to have a significant impact on $\delta^{15}N$ of aquatic primary consumers. Furthermore, the multiple regression analysis showed that each animal species contributed significantly and independently in elevating $\delta^{15}N$. However, loads originating from bovines tended to elevate primary consumer $\delta^{15}N$ faster than similar loads from pigs and poultry. This might be explained by differences in the storage and in the delay of incorporation of manure to fields. For example, Beaulieu (2004) showed that pig manure tended to be incorporated to fields more rapidly than bovine manure (38.5% of pig manure incorporated the same day it was produced versus 13.1% for bovine manure). Hence, bovine manure left on the surface might be exposed to larger volatilization rates and thus acquire higher $\delta^{15}N$ values than similar amounts of pig manure that have been injected to fields. Overall, the relationship obtained here shows how manure produced by different farm animals affects aquatic biota $\delta^{15}N$. In particular, our results could be used as a management tool to assess the relative impact of growth in the number of different livestock species (e.g., implantation of large pig factories) on the exportation of N to aquatic ecosystems.

Finally, curvilinear regressions were observed at all levels of analysis. Typically, $\delta^{15}N$ values showed little or no increases over a range of low levels of N loads. However, as N loads grew larger, $\delta^{15}N$ values started to increase disproportionately. This observation suggests that N loads are initially assimilated or immobilized by plants and soils, but as they further increase, soils become saturated and surplus of N are transformed and transported to rivers and lakes. The threshold at which $\delta^{15}N$ values started to increase faster (~300 kg N km^{-2} yr^{-1} for total anthropogenic N) corresponded to lightly developed watersheds having less than 5% of their area devoted to agriculture and/or less than 19 inhabitants km^{-2}. This suggests that, as watersheds go from lightly to moderately developed, N loads tend to rapidly exceed the immobilization capacity of soils and plants, and find their way to aquatic systems. The threshold up to which $\delta^{15}N$ values of aquatic consumers continue to increase as N loads grow larger remains unknown using the present study's results. Unfortunately, published studies examining the effects of N loads on aquatic biota $\delta^{15}N$ are generally characterized by moderate N loads and show $\delta^{15}N$ values similar to those estimated in the present study (e.g., McClelland and Valiela 1998; Chang et al. 2002; Mayer et al. 2002). However, studies of seabird rookeries, where total N inputs are considerable (e.g., 600 kg N d^{-1} in Lindeboom (1984); 738 kg N d^{-1} in Wainright et al. (1998)), and N transformation processes important, have shown surprisingly high $\delta^{15}N$ values in soils, plants and food webs associated with bird guano ($\delta^{15}N$ as high as 45‰; Mizutani et al. 1986; Mizutani and Wada 1988; Wainright et al. 1998; Barrett et al. 2005). Thus, we might expect larger $\delta^{15}N$ values than those reported here in watersheds where anthropogenic N loads are much larger.

In conclusion, $\delta^{15}N$ values of aquatic consumers were well related to total anthropogenic N loading intensity on the watershed. Similarly strong relationships were observed when loads from human population, synthetic fertilizers and livestock manure were analysed separately. However, $\delta^{15}N$ could not help to distinguish

unambiguously individual sources of N. Therefore our results suggest that $\delta^{15}N$ could be used as an effective indicator of N overloading of aquatic ecosystems, but not as a tracer of individual N sources.

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Table 1.1. Estimated amounts of nitrogen produced yearly by farm animals (kg N yr^{-1}).

Animal	Nitrogen produced (kg N yr^{-1})
Bovines	
Dairy Cow	83.89
Cow (beef)	70.63
Bull (beef)	80.05
Calf	14.48
Steer	47.09
Heifer	38.60
Pigs	
Piglet	1.99
Boars and sows	19.86
Fattening pig	9.86
Poultry	
Laying hen	0.33
Broiler chicken	0.18
Turkey	0.69

Calculations were made using animals of average weight. Yearly N amounts for broiler chickens were calculated for 275 days (lifespan of a broiler chicken), instead of 365 days as for other animals. All estimates are based on data provided by the Comité de références économiques en agriculture du Québec (1995).

Table 1.2. Relationships between N loads (kg N km^{-2} yr^{-1}) and $\delta^{15}N$ of primary consumers (PC; n = 79), predatory invertebrates (PI; n = 73) and fish (n = 62).

N Source	Consumer	r^2	a (s.e.)	b (s.e.)	c (s.e)	d (s.e)
Human	PC	0.46	3.80 (0.48)		1.06 (0.13)	
Human	PI	0.40	6.14 (0.46)		0.88 (0.13)	
Human	Fish	0.29	9.08 (0.61)		0.79 (0.16)	
Fertilizers	PC	0.62	3.50 (0.71)	0.28 (0.78)	0.60 (0.21)	
Fertilizers	PI	0.56	5.71 (0.68)	0.39 (0.77)	0.46 (0.21)	
Fertilizers	Fish	0.45	8.68 (0.50)		0.54 (0.08)	
Manure	PC	0.72	2.84 (1.09)	2.88 (2.24)	-1.65 (1.27)	0.42 (0.21)
Manure	PI	0.73	5.50 (0.94)	2.17 (1.95)	-1.43 (1.11)	0.39 (0.19)
Manure	Fish	0.62	6.84 (1.44)	4.92 (3.00)	-2.89 (1.66)	0.61 (0.27)
Total	PC	0.73	1.02 (2.07)	5.34 (3.60)	-2.81 (1.77)	0.57 (0.26)
Total	PI	0.70	7.36 (0.97)	-2.30 (0.88)	0.97 (0.19)	
Total	Fish	0.61	3.97 (2.68)	8.90 (4.70)	-4.55 (2.30)	0.80 (0.34)

Equation constants used for the regressions are shown as $y = a + b [\log (x+1)] + c [\log (x+1)]^2 + d [\log (x+1)]^3$. All relationships were highly significant ($p < 0.0001$). Total N shown here includes human population, fertilizer and livestock N, but excludes atmospheric deposition.

1.7. Figure Captions

Figure 1.1. Watersheds and stations (solid circles) sampled during summer 2000. Watersheds (clockwise): (a) Sainte-Anne, (b) Jacques-Cartier, (c) Etchemin, (d) Chaudière, (e) Bécancour, (f) Nicolet, (g) Saint-François, (h) Yamaska, (i) L'Assomption, (j) Maskinongé, (k) du Loup, (l) Saint-Maurice, (m) Batiscan.

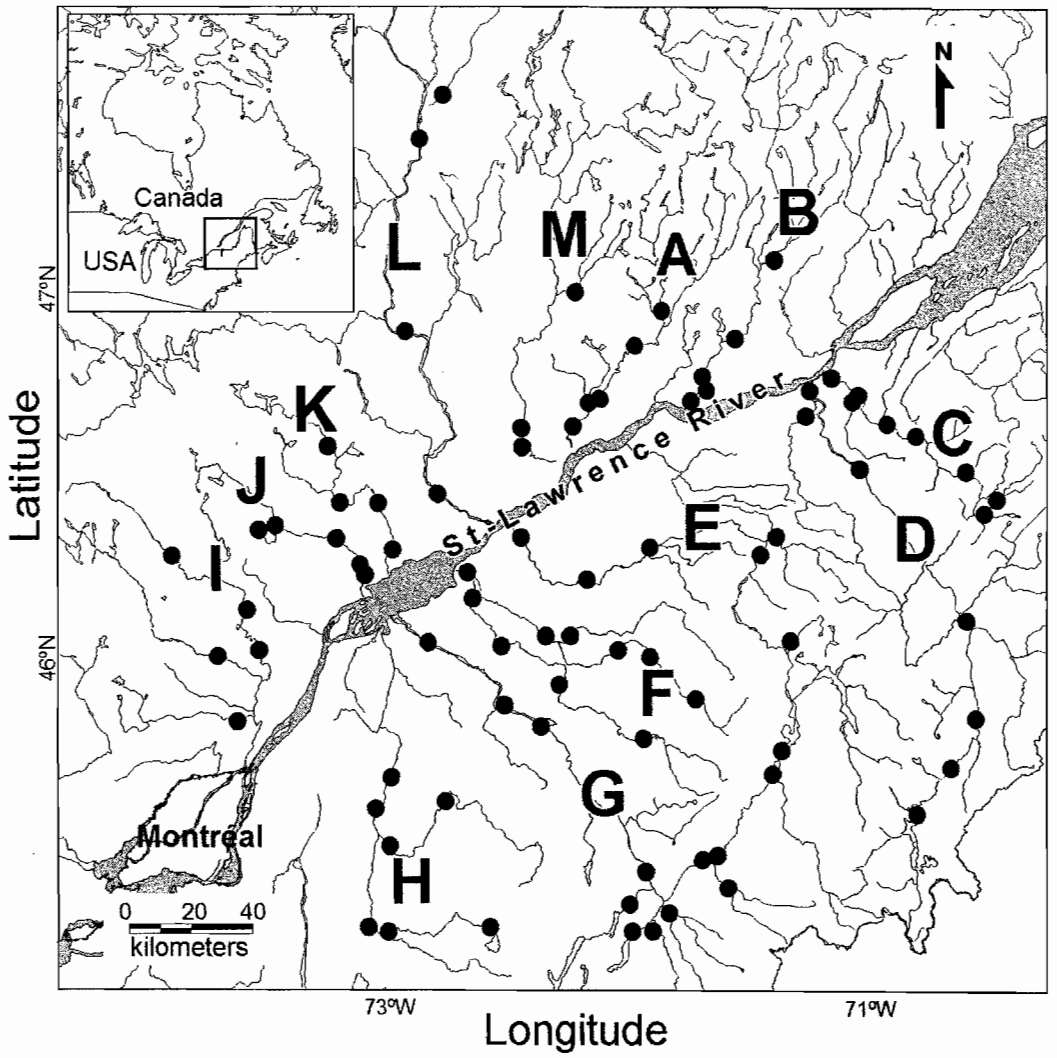
Figure 1.2. Relationships between a) livestock manure and human population N loads (kg N km^{-2} yr^{-1}; $r^2 = 0.69$; $p < 0.0001$) and b) livestock manure and synthetic fertilizer N loads (kg N km^{-2} yr^{-1}; $r^2 = 0.84$; $p < 0.0001$). The 1:1 relationships are represented by solid lines and the 10:1 relationships are represented by broken lines.

Figure 1.3. Relationships between mean $\delta^{15}N$ (‰) of a) primary consumers, b) predatory invertebrates, c) non piscivorous fish and anthropogenic N loads (kg N km^{-2} yr^{-1}; including livestock manure, synthetic fertilizers and human population). Regression coefficients and equations are shown in Table 1.2.

Figure 1.4. Relationships between mean primary consumer $\delta^{15}N$ (‰) and N loads (kg N km^{-2} yr^{-1}) originating from a) human population, b) synthetic fertilizers and c) livestock manure. Regression curves are illustrated with solid lines, while regression coefficients and equations are shown in Table 1.2.

Figure 1.5. Relationships between mean primary consumer $\delta^{15}N$ (‰) and N loads (kg N km^{-2} yr^{-1}) originating from a) bovines (regression line: $y = 4.06 - 0.68\ [\log (x+1)] + 0.78\ [\log (x+1)]^2$; $r^2 = 0.62$; $p < 0.0001$), b) pigs ($y = 5.26 + 0.37\ [\log (x+1)] + 0.41\ [\log (x+1)]^2$; $r^2 = 0.58$; $p < 0.0001$) and c) poultry ($y = 5.81 - 0.55\ [\log (x+1)] + 1.03\ [\log (x+1)]^2$; $r^2 = 0.38$; $p < 0.0001$). Regression curves are represented by solid lines.

Figure 1.6. Relationships between mean primary consumer $\delta^{15}N$ and percent contribution to total inorganic N load of a) human population b) synthetic fertilizers, and c) livestock manure N loads. Total inorganic N loads represent the sum of human population, synthetic fertilizers, livestock manure and atmospheric deposition N loads.


Canada
USA
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St-Lawrence River
Montreal
0 20 40
kilometers
47°N
46°N
73°W
71°W
Latitude
Longitude

Figure 1.1.

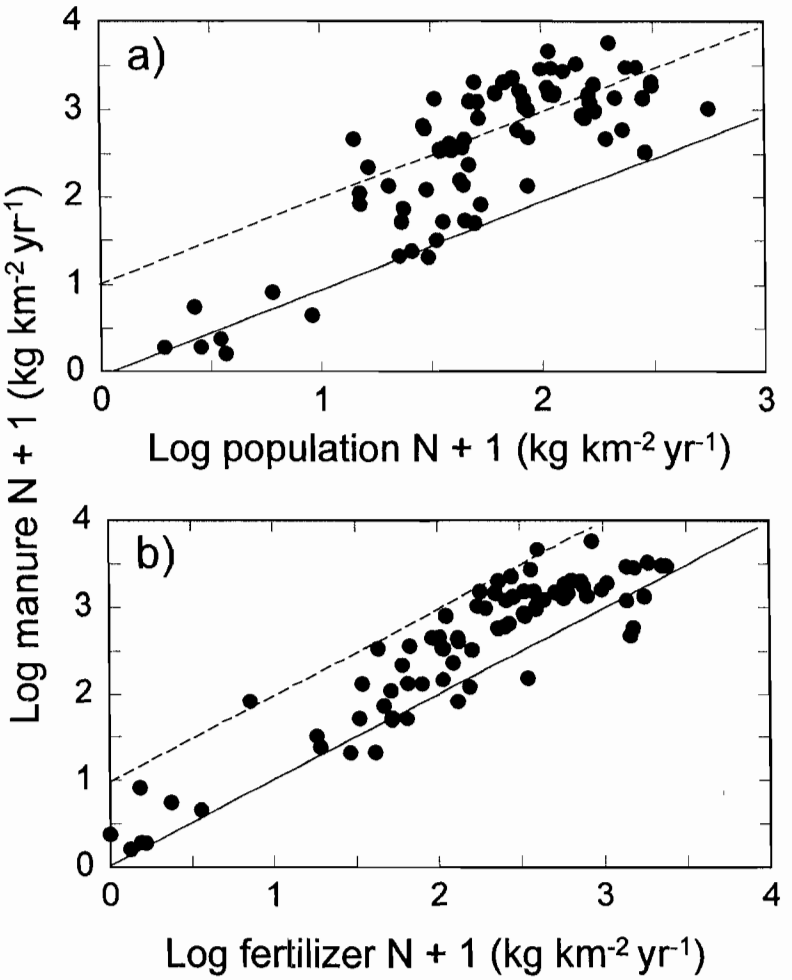
a)
b)
Log manure N + 1 (kg km-2 yr-1)
Log population N + 1 (kg km-2 yr-1)
Log fertilizer N + 1 (kg km-2 yr-1)
0
1
2
3
4

Figure 1.2.

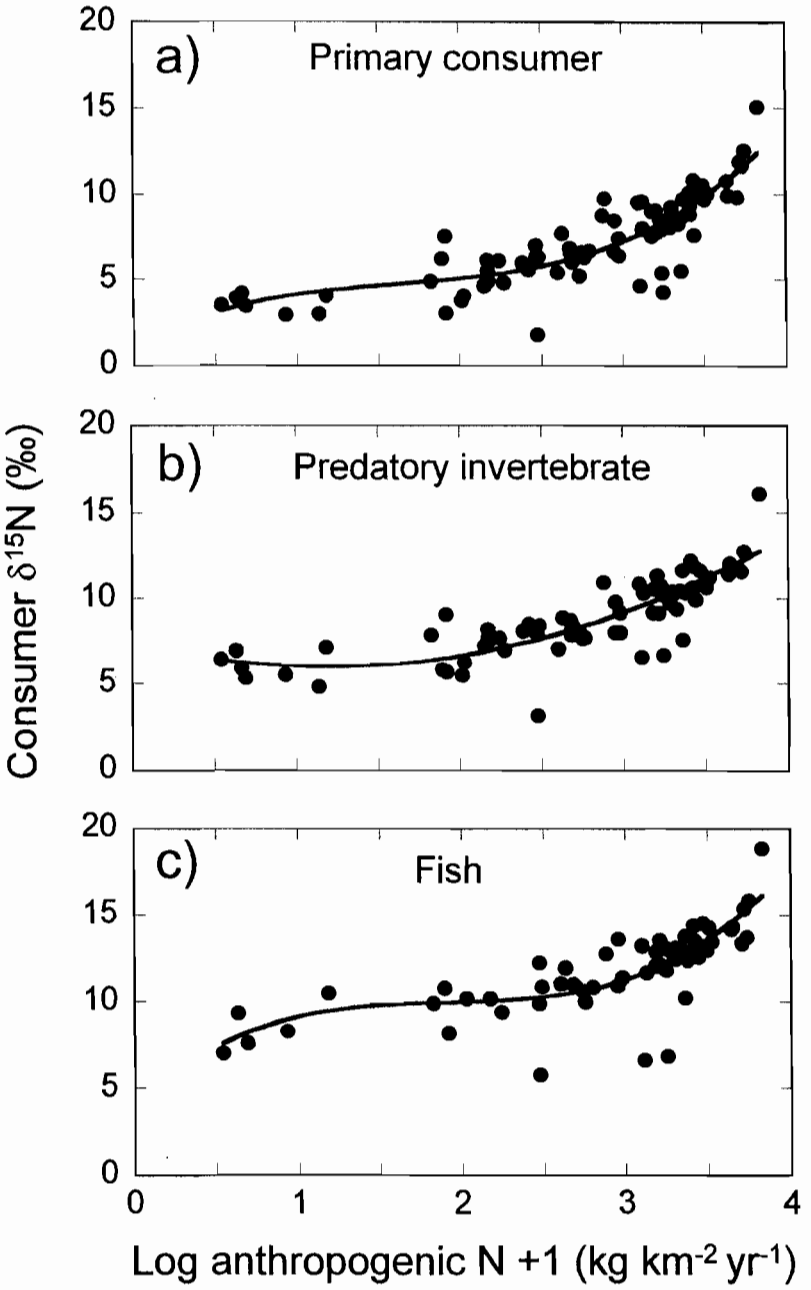
a)
Primary consumer
b)
Predatory invertebrate
c)
Fish
Consumer δ15N (‰)
Log anthropogenic N +1 (kg km-2 yr-1)
0
5
10
15
20
0
1
2
3
4

Figure 1.3.

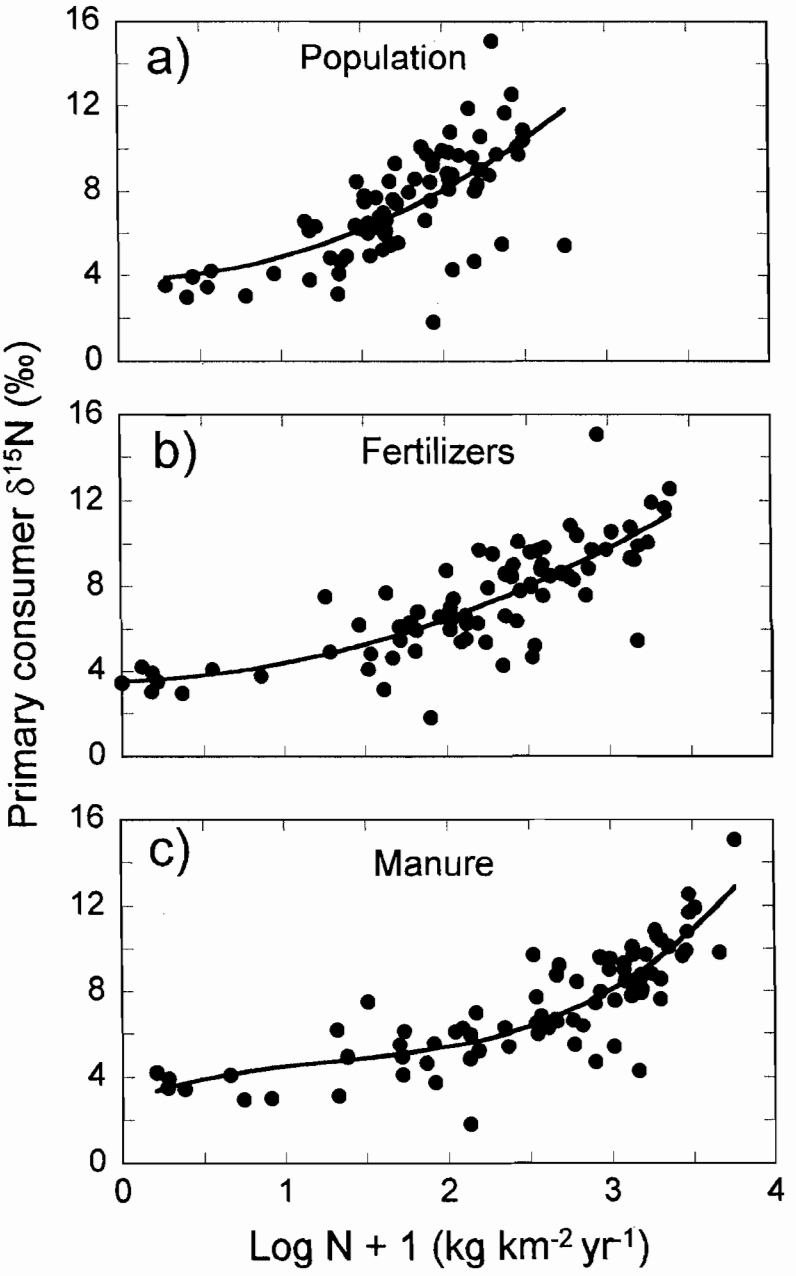
a)
Population
b)
Fertilizers
c)
Manure
16
12
8
4
0
0
1
2
3
4
Primary consumer δ15N (‰)
Log N + 1 (kg km-2 yr-1)

Figure 1.4.

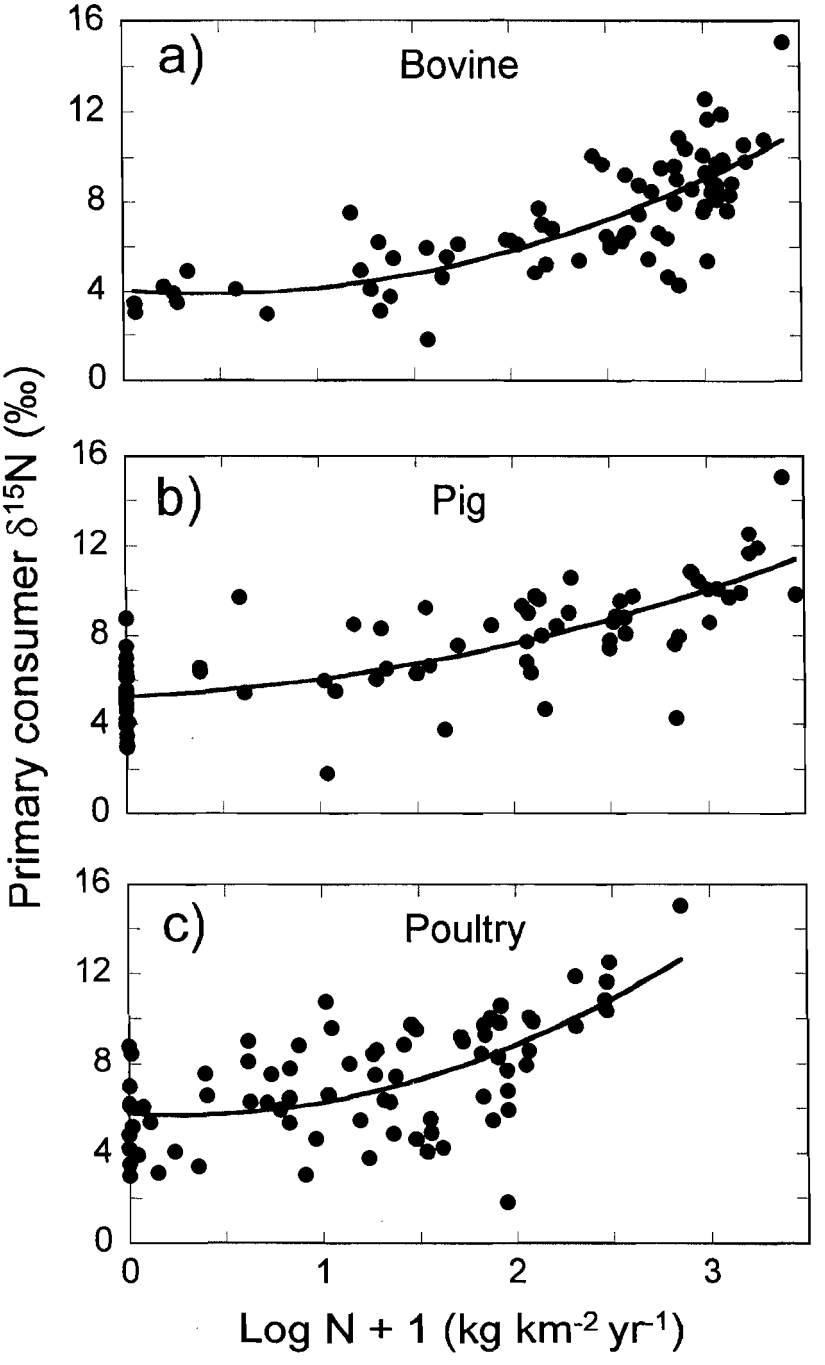
a)
Bovine
b)
Pig
c)
Poultry
Primary consumer δ15N (‰)
Log N + 1 (kg km-2 yr-1)
0
4
8
12
16
0
1
2
3

Figure 1.5.

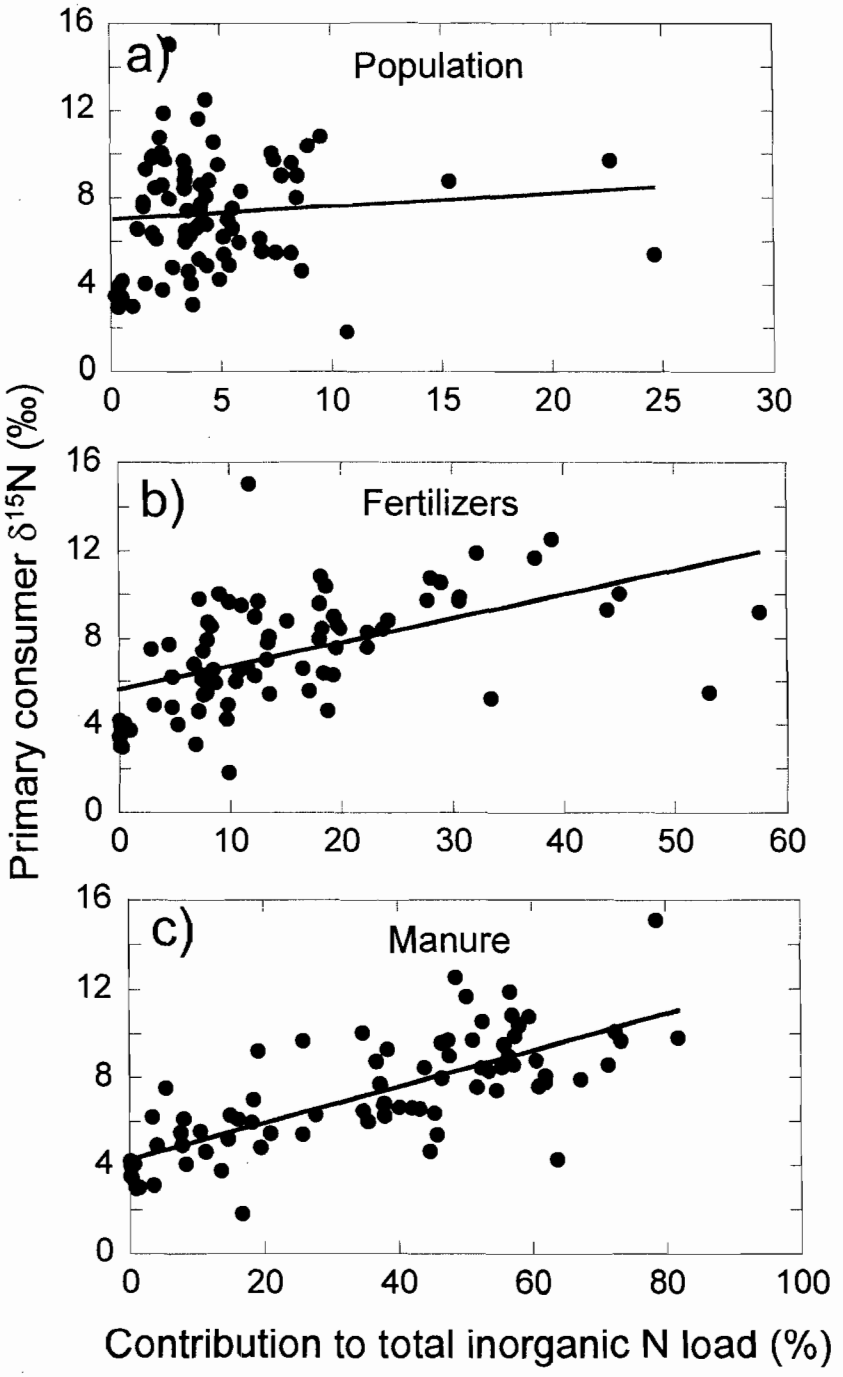
a)
Population
b)
Fertilizers
c)
Manure
Primary consumer δ15N (‰)
Contribution to total inorganic N load (%)
0
4
8
12
16
0
5
10
15
20
25
30
0
10
20
30
40
50
60
0
20
40
60
80
100

Figure 1.6.

CHAPITRE 2

ESTIMATION DE LA POSITION TROPHIQUE DES CONSOMMATEURS AQUATIQUES DES EAUX COURANTES À L'AIDE DES ISOTOPES STABLES D'AZOTE

ESTIMATING THE TROPHIC POSITION OF AQUATIC CONSUMERS IN RIVER FOOD WEBS USING STABLE NITROGEN ISOTOPES

Résumé

La variation intraspécifique et interspécifique de la position trophique des consommateurs est un élément central à plusieurs études portant sur le fonctionnement et la dynamique des écosystèmes. Depuis quelques années, de telles études emploient de plus en plus les isotopes stables de l'azote ($\delta^{15}N$) afin d'estimer la position trophique des consommateurs aquatiques. Cependant, lors de l'estimation de la position trophique à l'aide des isotopes d'azote, il importe de corriger le $\delta^{15}N$ de tout consommateur pour lequel on veut estimer la position trophique par le $\delta^{15}N$ d'un organisme situé à la base du réseau trophique (organisme de référence). Dans cette étude, nous discutons premièrement des étapes à suivre pour sélectionner un organisme de référence en rivière, où de nombreuses études isotopiques ont été réalisées, sans toutefois porter attention à l'identification de tels organismes. Nous avons d'abord examiné les différences intra-site dans le $\delta^{15}N$ des consommateurs primaires appartenant à divers groupes fonctionnels et taxonomiques et avons trouvé des différences significatives dans leur $\delta^{15}N$. En particulier, les collecteurs étaient significativement enrichis par rapport aux autres consommateurs primaires. Nous avons identifié les brouteurs comme organisme de référence parce qu'ils démontraient de faibles $\delta^{15}N$ et qu'ils étaient mieux distribués entre les sites d'étude que les autres consommateurs primaires. En employant ces organismes de référence, nous avons ensuite estimé les positions trophiques des consommateurs (invertébrés et petits poissons) pour 87 réseaux trophiques lotiques. Les consommateurs primaires présentaient une position trophique significativement plus faible (2,3) que les invertébrés prédateurs (2,9) et les poissons (3,5), valeurs qui concordaient avec celles présentées dans des études traditionnelles. Toutefois, les positions trophiques des consommateurs (invertébrés et poissons) étaient très variables entre les sites d'étude, l'écart-type de ces dernières s'étalant sur 0,67 niveaux trophiques, suggérant la présence d'omnivorie. La comparaison de ces positions trophiques avec celles basées sur le $\delta^{15}N$ moyen de tous les consommateurs primaires confondus (sans cibler les

brouteurs comme organismes de référence) a permis de conclure que, lorsque vient le temps d'estimer les positions trophiques, l'utilisation d'un nombre restreint de types d'organismes, accompagnée d'une correction des différences isotopiques entre les groupes utilisés, pourrait réduire les biais induits par l'utilisation de groupes fonctionnels divers dont le $\delta^{15}N$ est variable.

Abstract

Intraspecific and interspecific variation in the trophic position of various consumers is central to many theories of aquatic ecosystem functioning and dynamics. In recent years, such issues have been addressed using stable N isotopes ($\delta^{15}N$) to estimate trophic position of consumers in aquatic ecosystems. However, one needs to correct for variation in baseline $\delta^{15}N$ among sites to estimate the trophic position of any aquatic consumer using $\delta^{15}N$. We first discuss the steps needed to select a baseline indicator in river ecosystems, where abundant foodweb isotopic data have been published, but limited attention has been paid to identification of baseline organisms. We examined within-site differences in $\delta^{15}N$ among primary consumers belonging to different functional and taxonomic groups and found significant differences in $\delta^{15}N$. Collectors were significantly enriched compared to other primary consumers. We proposed scrapers as a baseline $\delta^{15}N$ indicator because they showed low $\delta^{15}N$ values and were more widely distributed than other primary consumers throughout our study sites. Using this baseline $\delta^{15}N$, we calculated continuous estimates of trophic position of consumers (invertebrates and small fish) for our 87 river food webs. Primary consumers had a significantly lower mean trophic position (2.3) than predatory invertebrates (2.9) and fish (3.5), results that are concordant with estimates based on traditional studies. However, trophic-position estimates of consumers (both invertebrates and fish) were highly variable across sites with standard deviations spanning up to 0.67 trophic levels, suggesting potential omnivory. Comparison of these trophic-position estimates with estimates based on mean $\delta^{15}N$ of all primary consumers combined (no targeting of scrapers as baseline indicators) suggests that using a constrained number of groups and correcting for isotopic differences among groups when estimating baseline $\delta^{15}N$ could reduce some biases induced by the use of various functional feeding groups with variable $\delta^{15}N$ values.

Key words: trophic position, stable nitrogen isotopes, lotic, invertebrates, fish, food webs.

2.1. Introduction

Foodweb structure provides a framework for ecological theories seeking to explain the abundance and dynamics of organisms belonging to different trophic levels (Hairston et al. 1960, Paine 1966, Fretwell 1977, Oksanen et al. 1981). In particular, variation in the trophic position of organisms is central to many theories of ecosystem functioning and dynamics (Morin and Lawler 1995, Post 2002, Power and Dietrich 2002). However, most traditional foodweb studies have been limited either to studies using discrete trophic positions that underestimated omnivory (e.g., Hairston et al. 1960, Oksanen et al. 1981, Persson et al. 1992) or to complex studies that required significant effort during sampling and identification to identify properly the trophic interactions among organisms (e.g., Paine 1966, Briand 1983, Goldwasser and Roughgarden 1993).

Stable N isotopes ($\delta^{15}N$) have been proposed as a powerful technique for measuring variation in consumer trophic position in a continuous manner (Fry 1988, Cabana and Rasmussen 1994, Vander Zanden et al. 1997). They take into account complex community structure such as omnivory and the presence of extra trophic levels below a focal consumer. $\delta^{15}N$ can be used to estimate the trophic position of consumers because consumers typically become enriched in ^{15}N relative to their food (average enrichment of 3.4‰ per trophic level; Minagawa and Wada 1984, Post 2002). However, $\delta^{15}N$ values of aquatic consumers vary greatly among systems not only as a function of their trophic position, but also as a result of spatial variation in $\delta^{15}N$ at the base of the food chain (Cabana and Rasmussen 1996, Hebert and Wassenaar 2001, Anderson and Cabana 2005, 2006). Therefore, correct measurement of trophic position using $\delta^{15}N$ necessitates selection of one or more organisms as a baseline against which consumer $\delta^{15}N$ can be compared (Cabana and Rasmussen 1996, Vander Zanden and Rasmussen 2001, Post 2002). Several studies have used

such an approach in lake ecosystems. For instance, Kling et al. (1992) revealed variable omnivory in a predatory copepod sampled in different ponds using differences in $\delta^{15}N$ between this predatory copepod and an herbivorous copepod. Cabana and Rasmussen (1994, 1996) showed similar among-system variation in the trophic position of pelagic forage fish and piscivorous fish using unionid mussel $\delta^{15}N$ as a baseline indicator (see also Vander Zanden et al. 1997, 2000). This approach also has been applied successfully to elucidate the importance of variation in fish trophic position to explain among-lake variation in fish contaminant concentration (Kidd et al. 1995) and to quantify impacts of the introduction of an exotic species on the foodweb structure of temperate lakes (Vander Zanden et al. 1999).

The application of the isotopic approach to the measurement of trophic position essentially has been limited to lacustrine systems. Little attention has been paid to riverine food webs despite the wealth of evidence pointing to the importance of energy flow and top-down processes in river and stream ecosystems (Obendorfer et al. 1984, Wooton and Power 1993, Power and Dietrich 2002). Finding an adequate baseline indicator can be difficult because the $\delta^{15}N$ of aquatic consumers can be highly variable and potentially is affected by factors such as functional feeding group, taxonomic group, and life stage (Branstrator et al. 2000, Zah et al. 2001, Vanderklift and Ponsard 2003). For instance, several primary-consumer functional feeding groups (e.g., collectors, scrapers, shredders) are found in lotic systems (Cummins and Klug 1979, Vannote et al. 1980). These functional groups can feed on different resources that show various $\delta^{15}N$ values that, in turn, can influence their $\delta^{15}N$. In addition, several taxonomic groups of putative primary consumers can show considerable omnivory, feeding on more than one trophic level (Anderson 1976, Parker and Voshell 1983, Plague et al. 1998). Thus, the indiscriminate use of any primary consumer as a $\delta^{15}N$ baseline indicator could be questionable. Consequently, differences in $\delta^{15}N$ among primary-consumer functional feeding groups and

taxonomic groups should be examined before establishing a protocol for baseline $\delta^{15}N$ selection.

Surveys of food webs have shown that omnivory is widespread in many different ecosystems (Polis 1991, Sprules and Bowerman 1988). Several detailed studies of individual species have shown, for example, that invertebrates can derive their energy from one or more trophic levels depending on context (Anderson 1976, Plague et al. 1998, Zah et al. 2001). These empirical observations are coherent with recent theoretical and experimental work showing that omnivorous species show more stable dynamics and, therefore, may persist longer than other secondary consumers (McCann and Hastings 1997, Holyoak and Sachdev 1998). In addition to omnivory, a species' trophic position may be changed by the addition or loss of other species occupying lower trophic levels. For example, the presence of the zooplanktivorous crustacean *Mysis relicta* and various pelagic forage fish in the pelagic food chain of certain lakes (because of natural biogeographic factors; Dadswell 1974) resulted in a higher trophic position for lake trout, the top predator present in these lakes. This lengthening of the path of energy through the food chain by intermediate-trophic-level consumers wedged into the food chain also resulted in increased biomagnification of contaminants in the top predator (Rasmussen et al. 1990, Cabana et al. 1994, Vander Zanden and Rasmussen 1996). Hence, among-system variation in the trophic position of consumers, sometimes in the lower echelons of the food chain, clearly has important bearings not only on the control of the abundance of lower trophic levels but also on patterns of energy flow and contaminant biomagnification in aquatic systems.

We examine and propose a method to select a lotic baseline $\delta^{15}N$ indicator. In particular, variation in $\delta^{15}N$ among functional and taxonomic groups of lotic primary consumers (potential baseline indicators) is examined and the organisms showing the

lowest $\delta^{15}N$ values (and, thus, potentially the lowest trophic position) and the broadest distribution are selected as our baseline indicators. This baseline $\delta^{15}N$ is used to estimate trophic position of lotic consumers in 87 river sites. Subsequently, our observations are compared with general trophic positions obtained in traditional studies. The variability in trophic position among and within functional and taxonomic groups is examined and the variability in apparent omnivory within and among these groups is surveyed. Last, trophic position estimates based on a selected baseline organism are compared with trophic positions calculated using mean primary-consumer $\delta^{15}N$ to reveal potential biases associated with the latter method.

2.2. Methods

2.2.1. Study sites

During the summer of 2000 (early June to late August) and 2003 (August), invertebrates and fish were sampled from riffles in 87 river sites located within 13 subwatersheds of the St. Lawrence River watershed (Fig. 2.1). Mean watershed area of the sites was 3556 km^2 (range = 32 km^2–42,820 km^2). Watersheds were characterized by varying landuse types and anthropogenic activities (Anderson and Cabana 2005, 2006). In 2001, 13% of these watersheds were heavily impacted by agricultural activities (>30% area devoted to tame or seeded pasture and cropland), 33% were mostly forested (<5% agriculture), and the remainder (54%) lay between these 2 extremes. Population density ranged from 0.2 to 127.1 inhabitants/km^2 (mean = 20.6).

2.2.2. Sampling and identification

Nonpredatory invertebrates (primary consumers) and predatory invertebrates were collected in 2000 and 2003 with a D-frame aquatic net. Fish were collected with D-frame nets in 2000 and by electrofishing in 2003. Samples were kept in coolers,

frozen within 8 h, and thawed for sorting and identification. Invertebrates were identified to family or genus and classified into 5 functional feeding groups (collectors [including collector-filterers and gatherer-collectors], filterers, omnivores, scrapers, and shredders) according to Merritt and Cummins (1996) and Thorp and Covich (1991). Fish were identified to species (Scott and Crossman 1974). Captured fish were small specimens of nonpiscivorous species (see table 1 in Anderson and Cabana 2005) or juvenile piscivorous fish such as smallmouth bass (*Micropterus dolomieui*) and rock bass (*Amplobites rupestris*). Their overall size (total length) ranged from 25 to 124 mm (mean = 68.1 mm, SD = 20.1 mm). Primary consumers were collected in 87 sites, predatory invertebrates in 76 sites, and fish in 69 sites.

All samples were dried at 60°C for ≥48 h and ground into a homogenous powder. Invertebrates were used whole for isotopic analyses. Single whole individuals were used in the case of large organisms (e.g., large predators), whereas smaller organisms were pooled by genus (Anderson and Cabana 2005). In the case of fish, small sections of muscle tissue were taken from individual fish and sent for isotopic analyses. Isotopic analyses were done at the University of New Brunswick with a Finnigan–Mat Delta Plus mass spectrometer. Overall, 1022 samples were used in our study. A total of 113 samples (including both study years) were analysed in duplicate and showed a mean SD of 0.17‰.

2.2.3. Baseline $\delta^{15}N$ and trophic-position estimates

The correlations and differences in $\delta^{15}N$ among primary-consumer functional feeding groups and taxonomic groups were examined to help identify an appropriate lotic baseline organism. The organism selected as our principal baseline indicator had the lowest $\delta^{15}N$ values among the functional and taxonomic groups examined (suggesting a lower trophic level) and had the broadest spatial distribution throughout

our study sites. This baseline $\delta^{15}N$ was used to estimate the trophic position of invertebrates and small fish based on the equation:

$$\text{Trophic position}_{\text{consumer}} = ([\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}}]/f) + 2 \qquad [1]$$

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value of the consumer for which the trophic position is estimated, $\delta^{15}N_{\text{baseline}}$ is the $\delta^{15}N$ value of the baseline organism, and 2 is the expected trophic position of the organism used to estimate baseline $\delta^{15}N$ (e.g., an herbivore). f is the fractionation factor expected between a predator and its direct prey and corresponds to ~1 trophic level. We used the 3.4‰ fractionation value proposed by Minagawa and Wada (1984) in their large field and laboratory study of ^{15}N fractionation among aquatic and terrestrial organisms. This fractionation value, also observed by Post (2002) in a subsequent empirical review, has been used in several studies estimating trophic position of aquatic consumers (e.g., Vander Zanden et al. 1997, Post et al. 2000).

In addition, trophic position of predatory invertebrates and fish was estimated using the mean primary-consumer $\delta^{15}N$ (all primary-consumer functional feeding groups combined by site) as a baseline $\delta^{15}N$. These estimates were compared with our initial trophic-position estimates (based on a limited number of taxonomic groups) to examine the effects on trophic position estimates of averaging $\delta^{15}N$ of multiple primary consumers vs using $\delta^{15}N$ values of a few selected organisms.

2.2.4. Statistical analysis

Data from 2000 and 2003 were combined for all statistical analyses. No site was represented more than once. Relationships among primary-consumer functional feeding group $\delta^{15}N$ and taxonomic-group $\delta^{15}N$ were examined using simple linear correlation analyses and paired *t*-tests (Zar 1999). Correlation analyses were used to

determine if $\delta^{15}N$ values were consistent among consumers across sites. In particular, they helped to confirm that the selected baseline organisms were well connected with the rest of the food web. For instance, scrapers and shredders feed on different resources (terrestrial vs aquatic) that might show contrasting $\delta^{15}N$ values across sites. If $\delta^{15}N$ values were different between these groups, the use of scrapers would be inappropriate in food webs mostly connected to the terrestrial pathway. Paired *t*-tests were done to identify mean differences in $\delta^{15}N$ among organisms throughout all 87 study sites. They helped to identify groups that were depleted in ^{15}N (probably herbivores) compared to others.

Analyses of variance (ANOVA) and Kruskal–Wallis tests (when assumptions concerning ANOVA could not be met; Zar 1999) were used to analyse the effects of functional feeding groups or taxonomic groups on the variability of trophic position of consumers. Trophic-position estimates of scrapers were removed from all trophic-position analyses because of data circularity ($\delta^{15}N$ of scrapers was used as baseline $\delta^{15}N$). Tukey multiple comparison tests and nonparametric multiple comparison tests (Zar 1999) were used to examine the differences in trophic position among trophic, functional, and taxonomic groups of aquatic consumers. Correlations between trophic-position estimates computed using different assumptions (baseline based on $\delta^{15}N$ values of selected organisms vs baseline based on mean $\delta^{15}N$ of all primary consumers) were examined using a model II linear regression (Legendre and Legendre 1998, Legendre 2001). All analyses were done using SYSTAT (version 8.00; SPSS, Chicago, Illinois) and SAS (version 8.0; SAS Institute, Cary, North Carolina).

2.3. Results

2.3.1. Variation in primary consumer $\delta^{15}N$

Mean $\delta^{15}N$ values of the 5 primary-consumer functional feeding groups analyzed were generally significantly and strongly correlated among study sites ($r > 0.72$, $p < 0.0001$) except relationships between shredders and filterers and between shredders and omnivores that had a small number of possible comparisons (≤ 3), limiting statistical tests. These results suggest that groups feeding on different resources (e.g., scrapers vs shredders) have similar $\delta^{15}N$ values from site to site. However, significant differences in $\delta^{15}N$ were observed between functional feeding groups of primary consumers (Table 2.1). Collectors were significantly enriched compared to scrapers, shredders, and filterers (paired t-test, $p < 0.05$).

Scrapers had significantly lower $\delta^{15}N$ values than collectors and were better represented than shredders or filterers throughout sampling sites. More precisely, scrapers were collected in 83% of sites, whereas shredders and filterers were captured in only 38% and 21% of sites, respectively. Therefore, we further examined scrapers as potential $\delta^{15}N$ baseline indicators. Significant differences in $\delta^{15}N$ were observed among scraper families (Table 2.2). Members from the Psephenidae (Coleoptera) had significantly lower $\delta^{15}N$ values than ephemeropterans classified as scrapers (Heptageniidae [*Heptagenia* and *Stenonema*] and Ephemerellidae [*Drunella*]), whereas gastropods (Physidae and Viviparidae) were not significantly different from other scrapers. Scraper size had a small but significant effect on scraper $\delta^{15}N$. Small organisms exhibited higher $\delta^{15}N$ values than larger organisms (difference between $\delta^{15}N$ values of individual scrapers and the lowest scraper $\delta^{15}N$ for each site vs size, $r_s = -0.42$, $p < 0.01$, $n = 37$). However, this trend was generated by differences in $\delta^{15}N$ among families. For instance, Ephemerellidae were smaller, on average, than Heptageniidae or Psephenidae, but showed significantly higher $\delta^{15}N$ values. When

families were examined separately, scraper size no longer had a significant effect on $\delta^{15}N$ ($p > 0.05$).

2.3.2. Estimation of baseline $\delta^{15}N$

Psephenids were chosen as our baseline indicators because they showed the lowest $\delta^{15}N$ values compared to other scrapers (suggesting little or no omnivory) and were well represented throughout the study sites. However, $\delta^{15}N$ values of other scraper families were included to yield baseline $\delta^{15}N$ for each study site because psephenids were not collected in all study sites. The $\delta^{15}N$ of other scraper families was corrected relative to the $\delta^{15}N$ values of psephenids to reduce potential biases related to the use of several scraper groups with variable $\delta^{15}N$ values. More precisely, the mean differences in $\delta^{15}N$ between Psephenidae and the other families of scrapers (Table 2.2) were subtracted from the mean $\delta^{15}N$ of the other families for each study site, when these differences were significant. For example, Ephemerellidae were significantly enriched, on average, by 2.4‰ compared to Psephenidae. Thus, 2.4‰ was subtracted from the mean $\delta^{15}N$ value of Ephemerellidae measured at each study site. The slopes of the $\delta^{15}N$ relationships among families were not significantly different from 1 (model II regression, Legendre 2001; 95% major axis slope confidence interval [CI] including 1), enabling the use of the mean difference. Overall, $\delta^{15}N$ values of scraper families with significantly higher $\delta^{15}N$ than Psephenidae (i.e., Ephemerellidae and Heptageniidae) were adjusted downward toward the $\delta^{15}N$ value of Psephenidae. The $\delta^{15}N$ values of the 2 gastropod families (Physidae and Viviparidae) were not used in the baseline estimates because these families were seldom collected and were not abundant enough to show any significant trend in $\delta^{15}N$ relative to other scrapers (paired *t*-tests; Table 2.2). Last, the corrected $\delta^{15}N$ values of the 3 remaining scraper families (Ephemerellidae,

Heptageniidae, and Psephenidae), if present, were averaged to yield baseline $\delta^{15}N$ for each study site.

2.3.3. Trophic-position estimates

2.3.3.1. Trophic positions of lotic consumers

Mean trophic position of lotic consumers was significantly different among the 3 broad trophic groups examined (1-way ANOVA, $F_{2,692} = 374.2$, $p < 0.0001$). Putative primary consumers had a mean trophic position of 2.31 (SD = 0.40), which was significantly lower than the mean trophic position of predatory invertebrates (mean = 2.88, SD = 0.40). Fish had a significantly higher trophic position (mean = 3.51, SD = 0.42) than both primary consumers and predatory invertebrates (Tukey multiple comparison test; Fig. 2.2).

Mean trophic position varied greatly among invertebrate primary-consumer functional feeding groups and taxonomic groups (Tables 2.3, 2.4). Functional feeding group had a significant effect on the trophic position of primary consumers (Kruskal–Wallis, $H = 24.59$, $p < 0.0001$, assuming χ^2 distribution with 3 df). Collectors had a significantly higher trophic position than shredders and omnivores (nonparametric multiple comparison tests, $p < 0.05$). Estimates of trophic position of nonpredatory invertebrates also varied significantly among taxonomic groups (Kruskal–Wallis; order effect: $H = 24.18$, $p < 0.0001$, 6 df; family effect: $H = 75.12$, $p < 0.0001$, 18 df). Mean trophic-position estimates of Gastropoda, Isopoda, Bivalvia, and Amphipoda were not significantly different from 2 (2-tailed t-test for difference between a population mean and a hypothesized population mean, $p > 0.05$; Zar 1999; Fig. 2.3A), suggesting a trophic position comparable to that of scrapers. Trophic-position estimates also varied among taxonomic groups of predatory invertebrates (Kruskal–Wallis; order effect: $H = 27.07$, $p < 0.0001$, 5 df; family effect: $H = 38.77$, $p < 0.0001$, 12 df). In particular, predatory Plecoptera (mostly composed of Perlidae) had

a higher mean trophic position than other predators (Fig. 2.3B). Mean trophic-position estimates of predatory invertebrate orders were all significantly >2 ($p < 0.05$). However, all orders showed estimates significantly <3 ($p < 0.05$), except predatory Plecoptera ($p > 0.05$).

Trophic position of fish also varied greatly among fish species and ranged from 2.22 to 4.54 trophic levels (Table 2.5). However, these estimates were not significantly different among the various fish species examined (1-way ANOVA, $p > 0.05$), even though some species tended to show lower mean trophic positions (e.g., *Notorus gyrinus*, *Lepomis gibbosus*) than others (*Cottus bairdi*).

2.3.3.2. Variability in trophic-position estimates

Trophic-position estimates within groups of invertebrates were, in general, highly variable. Standard deviations (estimated using trophic position of all consumers) spanned up to 0.67 trophic levels for individual families (Table 2.3) and from 0.30 to 0.60 trophic levels for functional feeding groups (Table 2.4). Shredders, in particular, had a highly variable apparent trophic position, ranging from 0.87 to 3.47. Variability in trophic position estimates of genera included in the examined families (when >1 genus was present in a family and $n \geq 5$; Table 2.3) were generally as variable for genera of a given family as they were for the whole family. Similarly, variability in trophic position estimates of fish was high, spanning up to 0.42 trophic levels for all fish species combined and up to 0.64 trophic level for individual species (Table 2.5).

2.3.3.3. Effect of baseline selection on trophic position

Mean trophic-position estimates of predatory invertebrates and fish (respectively averaged by sites) based on scraper $\delta^{15}N$ ($baseline_{scraper}$) were compared with estimates based on mean primary consumer $\delta^{15}N$ ($baseline_{pc}$; all primary-

consumer functional feeding groups combined) to identify potential biases associated with using mean indiscriminate $\delta^{15}N$ values of any primary consumer as baseline indicators. The 2 types of estimates were highly correlated ($r = 0.85$, $p < 0.0001$), but the estimates based on $baseline_{scraper}$ $\delta^{15}N$ tended to be higher than those based on $baseline_{pc}$ $\delta^{15}N$ (mean difference of 0.30 trophic level, $p < 0.0001$; Fig. 2.4). Furthermore, large differences of up to ~1 trophic level were observed between the 2 estimates (e.g., $baseline_{scraper}$ estimate of ~4.5 vs $baseline_{pc}$ estimate of ~3.5). The slope of the relationship was slightly, but significantly, >1 (mean slope of major axis = 1.19, 95% CI = 1.06–1.33), suggesting that higher trophic positions tended to be slightly more overestimated than smaller ones when using $baseline_{scraper}$ relative to $baseline_{pc}$.

2.4. Discussion

2.4.1. Variation in primary consumer $\delta^{15}N$

The $\delta^{15}N$ values of the 5 primary-consumer functional feeding groups examined were highly correlated. This result suggests that organisms feeding on different resources (e.g., terrestrial detritus vs periphyton) have similar $\delta^{15}N$ values. Shredders feed on terrestrial detritus, but previous studies have suggested that shredders assimilate their N from bacteria colonizing detritus rather than from the detritus itself (Newell 1965, Cummins and Klug 1979, Newell and Field 1983), and the bacteria derive their N from the aquatic system. Indeed, results from previous studies suggest that bacteria incorporate diverse elements from the surrounding aquatic system (dissolved minerals, organic and inorganic N, etc.), while assimilating the C of the detritus they colonize (Johannes and Satomi 1966, Wheeler and Kirchman 1986). Hence, detritivores feeding on bacteria living on detritus should show $\delta^{15}N$ values typical of the aquatic environment. Our results support this contention. Shredders have mean $\delta^{15}N$ values spanning from 1.9 to 10.6‰ across

sites, a higher range than that found for terrestrial detritus (e.g., ~–4‰ to +3‰ in Long-Term Ecological Research sites throughout the US; Fry 1991). Furthermore, $\delta^{15}N$ values of shredders were similar to those of scrapers, again suggesting that shredders derived their N from an aquatic food source. Overall, our results suggest that the use of scrapers in food webs mostly connected to the terrestrial pathway will still yield relevant trophic-position estimates, because both scrapers and shredders share similar $\delta^{15}N$ values.

Collectors had significantly higher $\delta^{15}N$ than other functional groups of primary consumers collected at the same sites. Zah et al. (2001) associated similar higher $\delta^{15}N$ values in collectors with the ingestion of animal food. Carnivory by collectors such as Hydropsychidae larvae has been well documented (Benke and Wallace 1980, Fuller and Mackay 1980, Parker and Voshell 1983) and could explain the higher $\delta^{15}N$ of the collector group in our study, which was largely composed of hydropsychids. Conversely, scrapers had low $\delta^{15}N$ values compared to collectors, an observation supported by Füreder et al. (2003), who observed lower $\delta^{15}N$ in scrapers compared to other presumed primary consumers in alpine streams. Significant differences also were found among scraper families, and these differences were potentially attributable to variability in their feeding behavior. For instance, the 2 mayfly families characterized as scrapers (Ephemerellidae [*Drunella*] and Heptageniidae [*Stenonema*, *Heptagenia*]) are facultative collectors, whereas members of the Psephenidae are adapted principally for scraping algae from rocks, and thus, are likely to show less omnivory (Hawkins 1984, Merritt and Cummins 1996, Voshell 2002). Consequently, the ability of these mayfly genera to collect particles of potential animal origin might explain their higher $\delta^{15}N$ compared to the less omnivorous psephenids.

2.4.2. Selection of a baseline indicator

As Post (2002) stated in an earlier study of baseline $\delta^{15}N$ selection in lakes, obtaining an appropriate baseline is one of the most difficult methodological issues facing the application of stable-isotope techniques to trophic foodweb analyses. Indeed, different techniques and a myriad of organisms may be used to derive baseline $\delta^{15}N$ estimates. In our study, using a restricted number of taxa (e.g., scrapers) as lotic baseline $\delta^{15}N$ indicators was proposed instead of using any primary-consumer assemblages. In particular, we suggest that, to choose a baseline organism properly, one should: 1) examine the differences in $\delta^{15}N$ among primary-consumer functional feeding groups and taxonomic groups, 2) select the organisms showing the lowest $\delta^{15}N$ values and the broadest spatial distribution for the type of ecosystems studied (e.g., shredders in small stream ecosystems vs scrapers in large rivers) as baseline indicators, 3) analyze and correct for size effects, if any, 4) correct for taxonomic differences in $\delta^{15}N$ if >1 organism is used, and 5) average the corrected $\delta^{15}N$ values to obtain the final baseline $\delta^{15}N$. We propose that using such an approach should reduce biases related to the use of various primary-consumer assemblages that can be heterogeneous across sites (e.g., composed of organisms with more or less elevated $\delta^{15}N$ values such as collectors vs scrapers). Indeed, an approach using the mean indiscriminate average $\delta^{15}N$ value of various primary consumers potentially could lead to erroneous conclusions about across-site variability in trophic position because invertebrate assemblages vary from site to site. In particular, variation in trophic position might reflect variability in the $\delta^{15}N$ of the types of organisms used in the baseline $\delta^{15}N$ instead of real changes in foodweb structure. Therefore, identifying the isotopic differences among the various consumers that can be used to estimate baseline $\delta^{15}N$ is an important step in selecting an appropriate lotic baseline indicator.

2.4.3. Trophic position

2.4.3.1. Trophic-position estimates of lotic consumers

Primary consumers, predatory invertebrates, and fish had mean trophic positions of 2.3, 2.9, and 3.5, respectively. These results mean that these groups were, on average, the equivalent of 1.3, 1.9 and 2.5 trophic levels, respectively, above primary producers. These results are fairly consistent with traditional food-chain models attributing trophic positions of ~1, 2, and 3, relative to primary producers, for herbivores, primary carnivores, and secondary carnivores (e.g., primary consumers, predatory invertebrates, and fish), respectively (e.g., Oksanen et al. 1981, Persson et al. 1992). Our results also are comparable with previous isotopic studies, in which invertebrates characterized as primary consumers typically showed lower $\delta^{15}N$ values than predatory invertebrates (Lancaster and Waldron 2001, Zah et al. 2001, Füreder et al. 2003), although some overlap was observed between primary consumer and predatory invertebrate $\delta^{15}N$ (as we also observed). Mean trophic position of fish was consistent with previous isotopic studies showing trophic positions of ~3 to 4 for small freshwater fish feeding mostly on invertebrates (Vander Zanden and Rasmussen 1996, Fry et al. 1999, Vander Zanden et al. 2000).

At a finer taxonomic scale, estimates of trophic position based on scraper $\delta^{15}N$ correctly identified families traditionally identified as being predatory but belonging to largely nonpredatory orders and vice versa. For example, Fuller and Stewart (1979) observed important consumption of animal matter by Perlidae and Perlodidae, 2 predatory Plecoptera, whereas Pteronarcyidae, a plecopteran shredder, ingested mainly detritus and moss. Our results are consistent with these observations, showing higher mean trophic positions for predatory stoneflies than for nonpredatory stoneflies (Table 2.3). Similarly, Slack (1936) documented how Rhyacophilidae, a predatory Trichoptera family, fed mainly on other aquatic insects, whereas other Trichoptera families remained much more herbivorous. Our trophic position

estimates of Trichoptera families, where Rhyacophilidae had higher mean trophic position than the other Trichoptera families, are concordant with this observation.

2.4.3.2. Omnivory and variability in trophic-position estimates

Mean trophic position of primary consumers was slightly >2, suggesting that primary consumers (collectors, shredders, filterers, and omnivores altogether) were, on average, slightly more carnivorous than scrapers. In particular, potential consumption of animal matter by collectors might have been responsible for this higher value. Mean trophic positions of predatory invertebrates and fish were slightly <3 (feeding exclusively on primary consumers, e.g., scrapers) and 4 (feeding exclusively on predatory invertebrates), respectively, which could also be attributable to omnivory. This observation is consistent with prior reports (e.g., Scott and Crossman 1974, Power 1990) showing that small fish can feed on both predatory invertebrates and primary consumers, as well as on primary producers. Similarly, gut-content analyses of predatory invertebrates have shown that several species ingest important amounts of algae and detritus (Thut 1969, Allan 1982) that could explain their trophic position being <3.

High among-site variability was found in trophic-position estimates of invertebrate taxonomic groups. This variability could be attributable, in part, to the identification level used (e.g., families or genera). For instance, variability in the trophic-position estimates of the invertebrate families examined could have been induced by variability in trophic position among the genera included in those families (high intergenus variability). This variability was observed, in part (Table 2.3); however, trophic-position estimates of individual genera were generally as variable as those found for the family to which they belonged, suggesting the presence of omnivory at lower taxonomic levels. Furthermore, we observed large variability in the trophic-position estimates of some families and genera that were expected to have specialized feeding behavior. For instance, our data suggested that shredders (e.g.,

Limnephilidae [Trichoptera] and Pteronarcyidae [Plecoptera], in particular) had highly variable trophic positions among sites. Plague et al. (1998) showed that Pteronarcyidae exhibited variable feeding behavior across sites, and fed on detritus, algae (diatoms), and animal matter. Thus, despite the fact that shredders traditionally are thought to feed mostly on detritus or microorganisms living on detritus (Cummins and Klug 1979), they can show quite variable feeding habits. Such feeding plasticity has been documented for several other aquatic invertebrates (Anderson 1976, Parker and Voshell 1983, Hawkins 1984, Friberg and Jacobsen 1994, Zah et al. 2001) and leads to the conclusion that omnivory is both important in aquatic systems and variable from system to system. Our results tend to support such a conclusion, showing large variations in trophic position of various taxonomic groups of invertebrates.

Trophic-position estimates of small fish (individual species) also were variable among sites, and spanned >1 trophic level. Large variability in fish trophic-position estimates (both forage and piscivorous fish) has been documented by Vander Zanden et al. (1997) and Fry et al. (1999) who attributed it to omnivory. The ability of fish to feed upon different trophic levels could, indeed, have caused such variability. For instance, Cabana and Rasmussen (1994) have found shifts of up to 1 trophic level in lake trout (*Salvelinus namaycush*) trophic position measured using $\delta^{15}N$ when they were feeding on herbivorous zooplankton, mysids, or forage fish. Thus, the ability to feed on primary producers, primary consumers, or secondary consumers (within or across sites) could explain the variability observed in the trophic-position estimates of fish species in the current study.

Variability in trophic position of forage fish among and within lakes observed in previous studies was comparable to the variability observed in our river network. For example, Vander Zanden et al. (2000) reported variation in trophic position of

invertebrate-feeding fish (including ciscos, littoral prey fish, and sculpins) of 2 trophic levels (~2.7–4.6) across 13 Canadian lakes. This variation was similar to the range observed in our study (~2.2–4.5). Other lake studies, however, have found slightly lower variability in trophic position of small insectivorous fish (~1 trophic level; Vander Zanden and Rasmussen 1996, Fry et al. 1999). Perhaps this difference is attributable, in part, to differences in feeding behavior and mobility of the fish species encountered in rivers compared to those found in lakes. For instance, long nose dace (*Rhinichthys cataractae*), a fish found in lotic systems but more rarely in lakes, showed a highly variable trophic position (2.64–4.54). Future studies comparing the degree of omnivory between lotic and lentic systems could give further insights into how these 2 systems differ.

Aside from feeding habits, differential assimilation and metabolic processes also might have generated the differences observed in $\delta^{15}N$ (and, thus, apparent trophic position) among or within the lotic consumer groups examined by inducing variable fractionation of ^{15}N (Vander Zanden and Rasmussen 2001, McCutchan et al. 2003, Vanderklift and Ponsard 2003). For instance, Jardine et al. (2005) showed that diet quality could generate variable fractionation of ^{15}N within and among invertebrate families collected in rivers, and this variability could lead to (spatially) variable trophic-position estimates. Jardine et al (2005) also showed that isotopic fractionation could vary among different functional feeding groups. In our study, variability in food quality at the base of the food web might have resulted in variable fractionation across sites, explaining the high variability observed in trophic-position estimates of invertebrates and fish. Similarly, variable fractionation among invertebrate functional feeding groups also could have generated the high variability observed in trophic-position estimates of invertebrate orders and families (which can be composed of >1 functional group). In addition, as Ponsard and Arditi (2001) suggested, different fractionation levels among species of invertebrates could also

contribute to the variability observed in trophic-position estimates (or $\delta^{15}N$ measurements) of invertebrate groups. In general, these studies question the use of a single fractionation value (e.g., 3.4‰) in trophic-position estimates because fractionation may vary greatly among different types of organisms or across sites. Although we used a single fractionation value, our results are concordant with literature, suggesting that the 3.4‰ fractionation value may be used to derive general conclusions about foodweb structure. Results found by Vander Zanden and Rasmussen (2001) support this contention. Indeed, Vander Zanden and Rasmussen (2001) found that error variances measured in consumer $\delta^{15}N$ at each trophic level (potentially attributable to variable fractionation) tended to cancel each other (decrease) at higher levels of the food chain, resulting in overall small error variances in higher-level consumer trophic-position estimates. However, Vander Zanden and Rasmussen (2001) observed an important effect of the type of baseline organism used (primary producers vs primary consumers) on the error variance of fractionation. These results suggest that selecting an adequate baseline organism might be more crucial to correctly estimating trophic positions than taking into account the variability in fractionation throughout the entire food web.

2.4.3.3. Effect of baseline selection on trophic position

Significant differences were found between trophic-position estimates based on $baseline_{scraper}$ $\delta^{15}N$ and estimates based on $baseline_{pc}$ $\delta^{15}N$. Trophic-position estimates based on $baseline_{scraper}$ $\delta^{15}N$ were higher than those based on $baseline_{pc}$ $\delta^{15}N$, a result attributable to the fact that $baseline_{scraper}$ $\delta^{15}N$ was based on low-$\delta^{15}N$ scrapers (downward adjusted towards Psephenidae). Both estimates were highly correlated, but high variability was observed in some cases. These differences might be attributable to the use of various primary consumers with variable $\delta^{15}N$ values in the $baseline_{pc}$. In addition, we found that higher trophic positions tended to be slightly more overestimated than smaller ones when using $baseline_{scraper}$ relative to $baseline_{pc}$.

This discrepancy could be attributed to error in calculating baseline $\delta^{15}N$ (either $baseline_{scraper}$ or $baseline_{pc}$). However, error in baseline estimates should have resulted in larger differences between smaller trophic positions because baseline $\delta^{15}N$ was subtracted from $\delta^{15}N$ values of consumers to estimate trophic position. Error in the fractionation value used could be a 2nd factor explaining the divergence in trophic-position estimates. For instance, Vander Zanden and Rasmussen (2001) obtained different fractionation levels and fractionation errors for carnivores and herbivores. Vander Zanden and Rasmussen (2001) also found that the type of baseline used can affect the error variance in fractionation for the whole food chain. In our study, we compared 2 baseline groups (scrapers vs all primary consumers) that might show contrasting fractionation levels or errors. In addition, we used a single fractionation value, which could lead to further errors in trophic-position estimates if fractionation changes at higher levels of the food chain. Such errors would lead to larger divergences when trophic position is high (as observed here) because the fractionation value is used as a denominator. Further examination of fractionation values and errors on trophic-position estimates could help clarify discrepancies such as those observed in our study.

In general, our results suggest that averaging $\delta^{15}N$ values of various primary consumers to estimate baseline $\delta^{15}N$ generally does not yield an important bias in trophic-position estimates relative to estimates based on scraper $\delta^{15}N$. However, caution should be used when comparing different primary-consumer groups or assemblages across sites because important differences were observed among functional groups of primary consumers and taxonomic groups of scrapers. For instance, one should avoid comparing trophic-position estimates based on collector $\delta^{15}N$ with estimates based on scraper $\delta^{15}N$ because these 2 groups have shown significant systematic differences in their $\delta^{15}N$. Overall, although the use of average primary-consumer $\delta^{15}N$ as baseline $\delta^{15}N$ generated trophic-position estimates

comparable to those obtained using scrapers only, we recommend either using a constrained number of baseline organisms, ubiquitous as much as possible and belonging to similar functional and taxonomic groups, or correcting for differences in $\delta^{15}N$ among groups when attempting to estimate trophic positions across several sites.

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Table 2.1. Mean paired differences in $\delta^{15}N$ (‰) among primary-consumer functional feeding groups (paired *t*-test). Mean enrichment in $\delta^{15}N$ is shown for the group in a row relative to the group in a column. Number of pairs (sites) is shown in parentheses. Significant differences ($p < 0.05$; Bonferroni corrected) are shown in bold.

	Collectors	Shredders	Filterers	Omnivores
Scrapers	**-0.5 (70)**	0.9 (27)	0.1 (14)	0.0 (20)
Collectors	–	**1.0 (32)**	**0.8 (17)**	0.6 (21)
Shredders		–	-0.8 (3)	-2.3 (2)
Filterers			–	-0.4 (12)

Table 2.2. Mean paired differences in $\delta^{15}N$ (‰) among families of scrapers (paired *t*-test). Enrichment in $\delta^{15}N$ is shown for the family in a row relative to the family in a column. Number of pairs (sites) is shown in parentheses. Significant differences ($p < 0.05$; Bonferroni corrected) are shown in bold. – indicates no pairs possible.

	Heptageniidae (*Heptagenia, Stenonema*)	Psephenidae	Physidae	Viviparidae
Ephemerellidae (*Drunella*)	**1.7 (13)**	**2.4 (11)**	–	–
Heptageniidae (*Heptagenia, Stenonema*)		**0.7 (24)**	-0.1 (3)	0.8 (5)
Psephenidae			-0.5 (2)	0.3 (3)
Physidae				-2.1 (2)

Table 2.3. Trophic-position estimates of aquatic invertebrates. Estimates are shown for each family. Estimates for genera are shown when >1 genus was present in the family and when the genus was represented by ≥5 organisms. Families and genera of scrapers used in the baseline $\delta^{15}N$ estimates have been excluded from orders and families shown here. NP = nonpredatory (primary consumer), P = predatory, *n* = total number of samples analyzed, SD = standard deviation.

Family	Genus	*n*	Mean	Min	Max	SD	Trophic Group
Amphipoda							
Gammaridae		15	2.17	1.14	2.86	0.48	NP
Anisoptera							
Aeshnidae		22	2.76	2.13	3.58	0.32	P
Cordulegastridae		3	2.73	2.55	2.96	0.21	P
Corduliidae		7	2.95	2.66	3.52	0.30	P
Gomphidae	All	33	2.85	2.25	3.82	0.39	P
	Ophiogomphus	26	2.81	2.25	3.82	0.33	P
Macromiidae		2	2.97	2.97	2.97	0.00	P
Bivalva							
Sphaeridae		11	2.04	1.70	2.53	0.26	NP
Unionidae		3	2.48	2.40	2.54	0.07	NP
Coleoptera							
Gyrinidae		8	2.65	2.42	2.93	0.16	P
Ephemeroptera							
Ephemerellidae		1	2.11	2.11	2.11	-	NP
Ephemeridae		7	2.45	2.26	2.72	0.17	NP
Heptageniidae		15	2.38	1.78	3.05	0.32	NP
Isonychiidae		37	2.19	1.59	2.76	0.28	NP

Neoephemeridae		1	1.96	1.96	1.96	-	NP
Polymitarcyidae		18	2.25	2.02	2.50	0.14	NP
Potamanthidae		2	1.97	1.81	2.12	0.22	NP
Gastropoda							
Physidae		3	2.20	2.14	2.28	0.07	NP
Planorbidae		2	2.64	2.38	2.90	0.37	NP
Viviparidae		5	1.78	1.50	2.05	0.20	NP
Isopoda							
Asellidae		9	2.09	1.68	3.04	0.40	NP
Megaloptera							
Corydalidae	All	29	2.70	2.04	3.83	0.36	P
	Corydalus	5	2.70	2.37	3.11	0.27	P
	Nigronia	21	2.62	2.04	3.03	0.29	P
Sialidae		2	3.22	3.22	3.22	0.00	P
Plecoptera							
Perlidae	All	85	3.05	2.02	3.99	0.43	P
	Acroneuria	27	2.91	2.06	3.85	0.33	P
	Agnetina/ Paragnetina	55	3.14	2.13	3.99	0.43	P
Perlodidae		1	2.83	2.83	2.83	-	P
Pteronarcyidae		18	2.22	1.04	3.19	0.46	NP
Trichoptera							
Brachycentridae		2	2.21	1.74	2.68	0.67	NP
Hydropsychidae	All	135	2.46	0.68	3.24	0.38	NP
	Ceratopsyche/ Hydropsyche	90	2.50	0.68	3.24	0.41	NP
	Chematopsyche	19	2.34	1.90	2.75	0.25	NP
	Macrostemum	12	2.27	1.88	2.75	0.26	NP
Lepidostomatidae		1	2.48	2.48	2.48	-	NP

Limnephilidae		16	1.88	0.87	3.47	0.66	NP
Philopotamidae	All	44	2.26	1.45	3.07	0.28	NP
	Chimarra	33	2.26	1.45	2.79	0.27	NP
	Dolophilodes	10	2.24	1.88	3.07	0.35	NP
Polycentropodidae		3	2.50	2.30	2.72	0.22	NP
Rhyacophilidae		43	2.81	1.19	4.28	0.51	P
Zygoptera							
Calopterigidae		2	2.21	1.92	2.50	0.41	P
Coenagrionidae	All	15	2.85	2.25	3.40	0.39	P
	Argia	5	3.08	2.68	3.40	0.34	P
	Enallagma	5	2.76	2.25	3.38	0.43	P

Table 2.4. Trophic-position estimates of invertebrate functional feeding groups (nonpredatory and predatory). *n* = total number of samples analyzed, SD = standard deviation, 95% CI = confidence interval.

Functional group	n	Mean	Mininum	Maximum	SD	95% CI
Collector	265	2.37	0.68	3.24	0.35	±0.69
Filterer	14	2.13	1.70	2.54	0.30	±0.65
Omnivore	24	2.14	1.14	3.04	0.44	±0.9i
Shredder	35	2.07	0.87	3.47	0.60	±1.22
Predatory invertebrate	252	2.88	0.81	4.28	0.42	±0.83

Table 2.5. Trophic-position estimates of fish species. *n* = the total number of individual fish analyzed, SD = standard deviation.

Species	n	Mean	Minimum	Maximum	SD
Amplobites rupestris	2	3.29	3.12	3.46	0.24
Catostomus commersoni	4	3.51	2.98	4.04	0.46
Cottus bairdi	2	4.08	3.74	4.41	0.47
Etheostoma flabellare	7	3.65	3.04	4.06	0.43
Etheostoma nigrum	13	3.36	2.56	4.23	0.41
Exoglossum maxillingua	4	3.53	2.93	4.08	0.47
Fundulus diaphanus	2	3.91	3.86	3.96	0.07
Lepomis gibbosus	3	4.95	2.22	3.38	0.64
Micropterus dolomieui	3	3.38	2.87	4.07	0.62
Notropis sp.	4	3.43	2.95	3.86	0.39
Noturus flavus	6	3.40	3.22	3.72	0.18
Noturus gyrinus	1	2.69	2.69	2.69	-
Percina caprodes	8	3.59	2.97	4.12	0.40
Rhinichthys atratulus	7	3.72	3.32	4.08	0.30
Rhinichthys cataractae	37	3.55	2.64	4.54	0.40
Total	103	3.51	2.22	4.54	0.42

2.7 Figure Captions

Figure 2.1. Study sites in the St. Lawrence River watershed (see Anderson and Cabana 2005, 2006 for further details).

Figure 2.2. Box plots of trophic-position estimates of primary consumer (PC), predatory invertebrates (PI), and fish. Boxes show the interquartile range and whiskers show the 10^{th} and 90^{th} percentiles. The median value is shown as a horizontal line in the middle of the box and the open circles mark outliers. Scrapers used in the baseline $\delta^{15}N$ estimates were excluded. Groups are sorted by ascending mean trophic position. Bars with the same letter are not significantly different (Tukey multiple comparisons tests, $p > 0.05$).

Figure 2.3. Box plots of trophic-position estimates of nonpredatory (A) and predatory (B) invertebrate orders. See Fig. 2.2 for explanation of the box plots. Scrapers used in the baseline $\delta^{15}N$ estimates were excluded from the groups shown here. Bars with the same letter are not significantly different (nonparametric multiple comparison tests, $p > 0.05$). Significant differences in trophic position among groups are shown separately for nonpredatory (Roman letters) (A) and predatory orders (Italic letters) (B). Groups are: Amphipoda (Amp), Anisoptera (Ani), Bivalvia (Biv), Coleoptera (Coleo), Ephemeroptera (Eph), Gastropoda (Gas), Isopoda (Iso), Megaloptera (Meg), Plecoptera (Pleco), Trichoptera (Trich), and Zygoptera (Zyg).

Figure 2.4. Relationship between trophic-position estimates of predatory invertebrates and fish based on scraper $\delta^{15}N$ ($baseline_{scraper}$) and estimates based on mean $\delta^{15}N$ of all primary consumers ($baseline_{pc}$). The regression equation (model II, major axis) is $y = -0.25 + 1.19x$. The dashed line shows a 1:1 relationship.

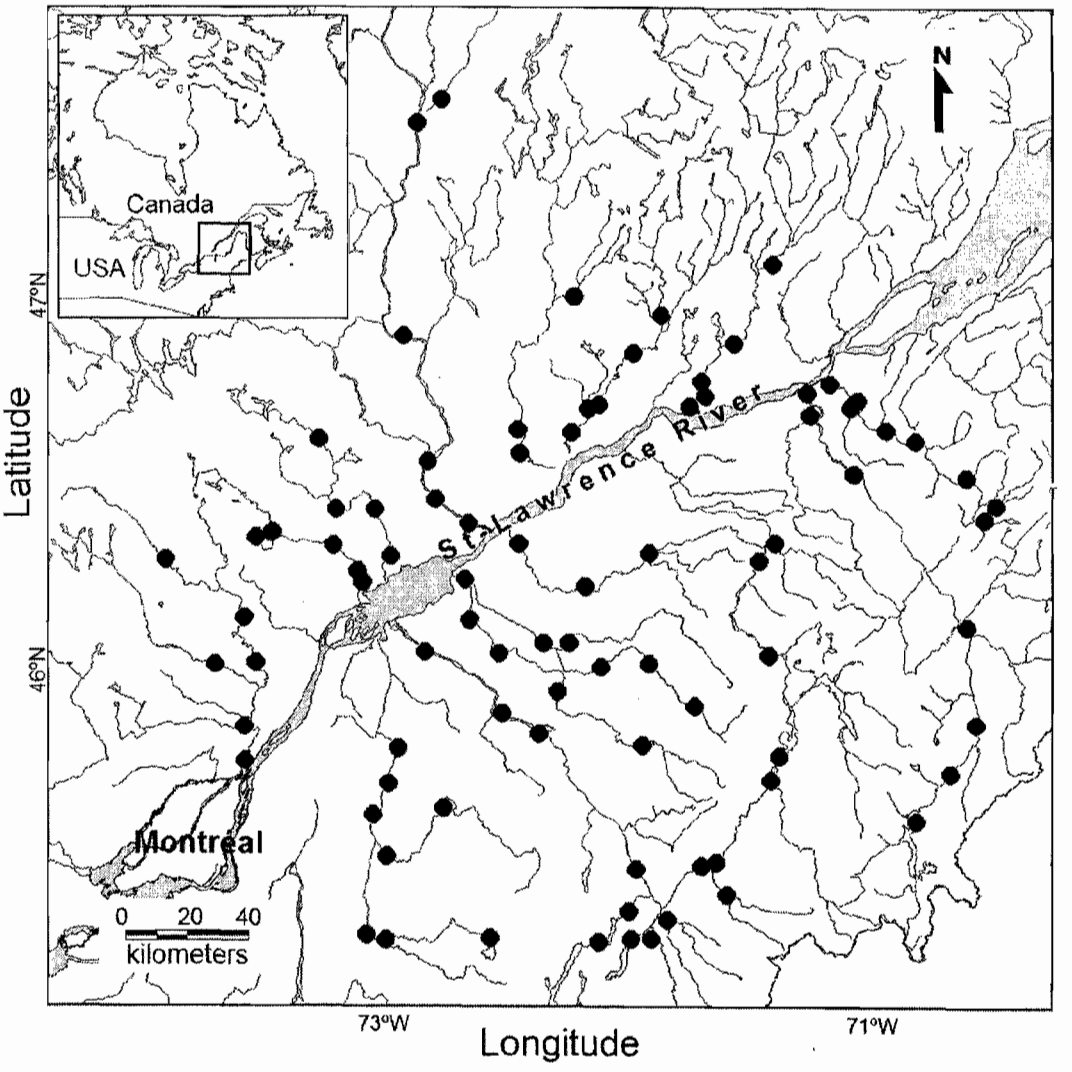
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Figure 2.1.

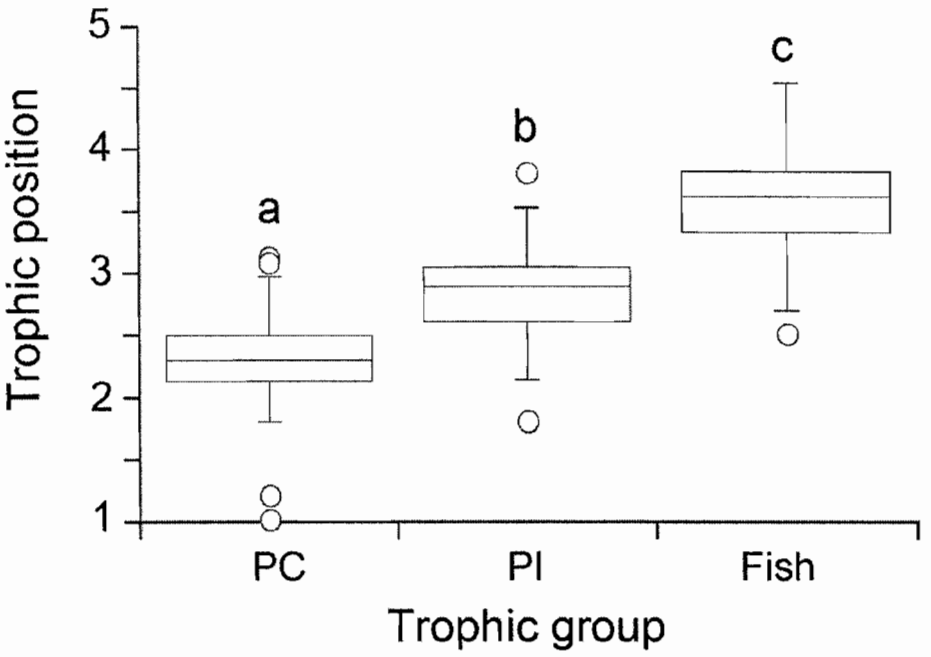
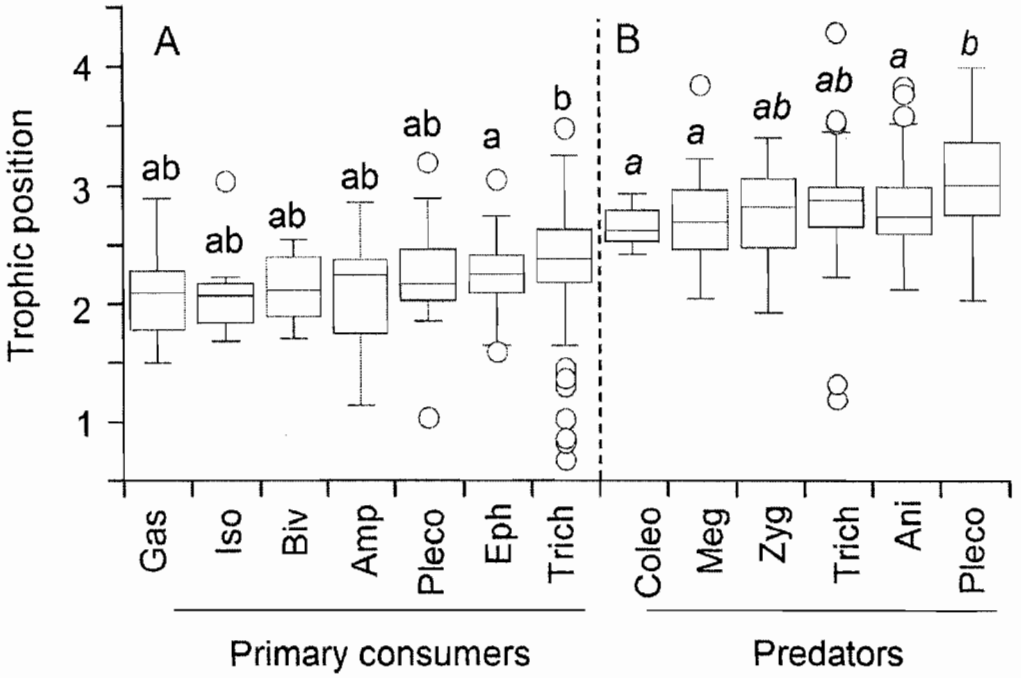


Figure 2.2.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Coleo
Meg
Zyg
Trich
Ani
Pleco
Primary consumers
Predators

Figure 2.3.

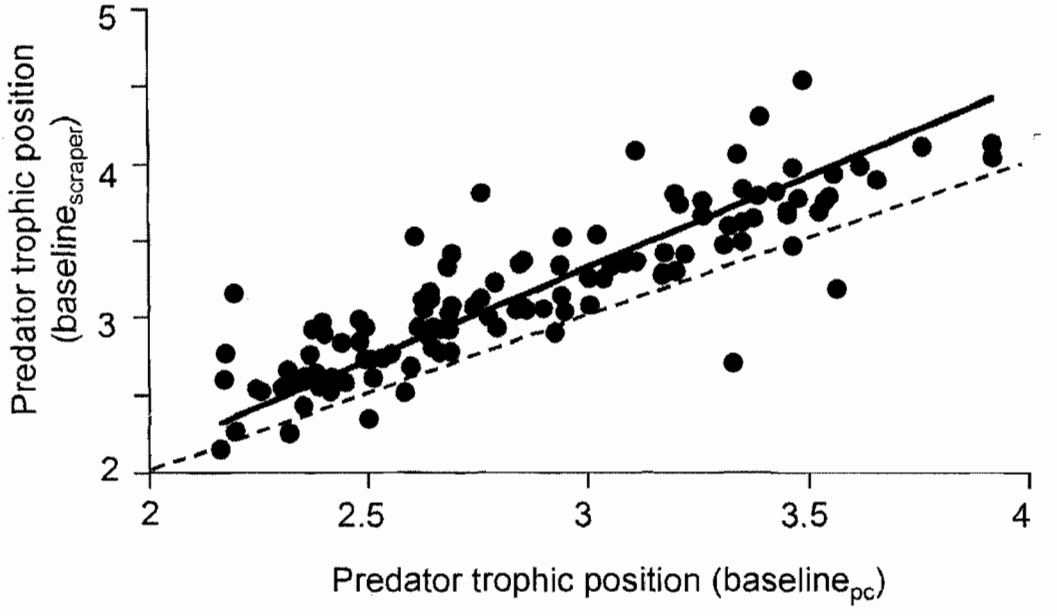
Predator trophic position (baseline$_{scraper}$)
5
4
3
2
2
2.5
3
3.5
4
Predator trophic position (baseline$_{pc}$)

Figure 2.4.

CHAPITRE 3

PRÉDIRE LA DENSITÉ DES COMMUNAUTÉS LOTIQUES À L'AIDE DE LA PRODUCTIVITÉ DU MILIEU ET DE LA POSITION TROPHIQUE

PREDICTING DENSITY IN LOTIC COMMUNITIES USING SYSTEM PRODUCTIVITY AND TROPHIC POSITION

Résumé

Les distributions densité-taille des organismes ont été largement employées afin de mieux comprendre et d'identifier des généralités dans la structure des communautés aquatiques et terrestres. Plusieurs études antérieures ont révélé que la taille était fortement corrélée à la densité animale. Cependant, d'importantes variations dans la densité à l'intérieur d'une classe de taille donnée étaient tout de même observées, menant à la conclusion que d'autres facteurs tels que le niveau trophique des organismes pourraient aussi affecter la densité. Dans cette étude, nous examinons si la variation dans la densité d'invertébrés lotiques appartenant à différentes classes de taille peut être expliquée par des changements dans la productivité, la température et la position trophique. Ni la position trophique ni la température n'expliquaient de façon significative la variation dans la densité des différentes classes de taille ($p > 0.05$). Cependant, la chlorophylle *a*, liée à la productivité, expliquait une fraction de la variation dans la densité pour deux des plus grosses classes de taille. Une régression multiple portant sur toutes les classes de taille simultanément permit d'observer que la taille expliquait 47% des changements dans la densité des invertébrés, tandis que la chlorophylle *a* et l'azote total expliquaient ensemble 9% de plus de cette variabilité. L'absence de relation entre la densité et la position trophique n'est pas concordante avec les études antérieures qui ont démontré que les herbivores maintiennent généralement de plus hautes densités que les carnivores de même taille. De plus, le très faible effet de la productivité suggère que d'autres facteurs tels que la prédation, la complexité de l'habitat ou les perturbations joueraient un rôle plus important sur la densité des invertébrés lotiques.

Abstract

Density-size distributions of organisms have been widely used to understand and report generalities in the structure of aquatic and terrestrial communities. Previous studies found that size was an important predictor of animal density. However, large variations in density for a given size class remained, and led to the conclusion that other factors such as the trophic level of organisms could also affect density. In this study, we examine if variation in density of lotic invertebrates of different size can be explained by changes in trophic position, productivity and temperature. Chlorophyll *a* (productivity) explained a fraction of the variation in density in two of the largest size classes. Trophic position did not explain changes in density within size classes, nor did temperature ($p > 0.05$). Using all size classes, we found that size explained 47% of invertebrate density, while chlorophyll *a* and total N accounted for an additional 9%. The lack of relationship between density and trophic position does not agree with previous studies showing that herbivores maintain higher densities than carnivores for a given size class. Further, the small effect of productivity suggests that other factors such as predation, habitat complexity or disturbance might play a greater role on lotic invertebrate density.

Key words: Density, Invertebrate, Lotic, Productivity, Nitrogen isotopes, Temperature, Trophic position.

3.1. Introduction

Predicting animal abundance and identifying the factors influencing it is one of the fundamental goals of ecology (e.g., Andrewartha and Birch 1961; Elton 1971; Damuth 1981). Among the variables investigated, body size has proved to be a simple yet powerful predictor of animal abundance. Across a wide range of terrestrial and aquatic habitats and species, total population density has been shown to significantly decrease with body size (Damuth 1981; Peters and Wassenberg 1983; Cyr et al. 1997a; Cohen et al. 2003; Brown et al. 2004). However, substantial variability in density within size classes remained, suggesting that other factors than size influence density. The non-linearity observed in many density-size relationships and the presence of several peaks and troughs throughout the size spectrum (e.g., Mercier et al. 1999; Havlicek and Carpenter 2001; Solimini et al. 2005) also suggest that these other factors have varying impacts on different size classes.

Several community and environmental attributes may explain variation in density within particular size classes. In particular, two types of factors might explain such variation: 1) bottom-up factors related to available resources (system productivity) and diffusion of energy up the food web; 2) top-down factors such as predation. In this study, we concentrate on bottom-up factors. Productivity is a first bottom-up factor that might influence the density of aquatic communities. Greater productivity at the base of the food web is expected to yield more energy (e.g., food supply) which will in turn support greater densities of consumers. This hypothesis is supported by several studies which have found higher densities of aquatic invertebrates in fertilized systems than in unfertilised (control) ones (Hart and Robinson 1990; Sardá et al. 1996; Perrin and Richardson 1997). However, Cyr et al. (1997b) found that variation in productivity did not have the same impact on small and large aquatic organisms (including phytoplankton, zooplankton,

macroinvertebrates and fish). They found that the density of small species increased more with increasing productivity than did the density of larger species. Thus, we might expect to find higher overall densities in more productive systems, but also greater increases in the densities of smaller organisms compared to large ones. The slopes of density-size relationships may therefore be affected by productivity.

A second factor that might affect aquatic community density is water temperature. Biological activity and growth rates generally increase with temperature, at least within the temperature range of normal activity (~0-40°C; Cossins and Bowler 1987; Gillooly et al. 2001; Brown et al. 2004). Several laboratory studies have found shorter developmental times for aquatic invertebrates and fish held at warmer temperatures (e.g., Sweeney 1984; Gillooly 2000; Gillooly et al. 2002). In the field, annual invertebrate production has been found to increase with mean annual temperature in stream (Morin and Bourassa 1992) and lake (Plante and Downing 1989) ecosystems. Moreover, higher temperatures might also enhance the quantity and the quality of food (e.g., greater productivity of periphyton and faster development of microbial populations on detritus; Sweeney 1984). For these reasons, we might expect higher invertebrate densities in warmer systems. Temperature might also affect differently the density of small versus large organisms. First, higher temperatures might raise the density of smaller organisms faster than larger ones, because small organisms usually have faster rates of increase (Hennemann 1983; Gillooly et al. 2001; Savage et al. 2004). Conversely, warmer temperatures, by speeding up larval growth, might yield greater numbers of larger and more mature individuals (Sweeney 1984; Hellawell 1986).

The trophic position of organisms could be a third factor associated with bottom-up processes explaining variation in density within a given size class. Following the energetic efficiency hypothesis, predators should be less abundant than

herbivores of the same size because of energetic inefficiencies in the transformation of energy with increasing trophic level (Lindeman 1942; Slobodkin 1963; Kerr and Dickie 2001). Hence, greater proportions of predators in a given size class should result in lower densities. Several studies on mammal density support this hypothesis. In a recent review examining the relationship between mammal body size and density, Brown et al. (2004) observed considerable variability in the densities of mammals of similar size. They attributed part of this variation to variability in trophic position of mammals. In particular, they found that populations of herbivorous mammals maintained much higher densities than did carnivorous species of the same size.

Most studies that have examined the effects of trophic position on animal density have either been limited to the study of large animals with known feeding habits (e.g., mammals: Damuth 1981; Peters and Raelson 1984) or have computed trophic positions using stomach content or connectance analyses (Cohen et al. 2003), which are time-consuming and yet may underestimate omnivory. In aquatic systems, where organisms are small and omnivory is widespread (Sprules and Bowerman 1988; Plague et al. 1998; Anderson and Cabana 2007), the estimation of trophic positions can be time-consuming and may require a high level of taxonomic expertise. Stomach contents of many invertebrates may also be difficult to identify and differential assimilation of different types of prey may bias estimated trophic positions (Cummins 1973). Stable nitrogen isotopes ($\delta^{15}N$) could alleviate these problems with the estimation of trophic position by providing a general quantitative approach applicable to all size classes of organisms. $\delta^{15}N$ values offer realized estimates of trophic positions of consumers because they take into account complex food web interactions such as omnivory (Cabana and Rasmussen 1994; Vander Zanden et al. 1997; Post 2002). Previous isotopic studies have used $\delta^{15}N$ values to examine trophic position-size relationships in aquatic communities (France et al.

1998; Jennings et al. 2002). However, no study to our knowledge has attempted to relate variability in density of aquatic organisms within size classes with changes in trophic position estimated using stable nitrogen isotopes. Moreover, most isotopic studies have examined $\delta^{15}N$-size relationships using $\delta^{15}N$ of individual species (France et al. 1998; Branstrator et al. 2000; Deudero et al. 2004). The use of an ataxonomic approach (estimating mean trophic position of the biomass of a given size class irrespective of the types of organisms comprised in it) may lead to more general conclusions on how overall (average) food web structure is influenced by various abiotic and biotic factors. The use of such an approach is supported by Jennings et al. (2001). They found that weak cross-species relationships between body size and $\delta^{15}N$ of fish (when species were examined individually) became highly significant when species were pooled by size class. Thus, pooling organisms by size class (combining size and $\delta^{15}N$ values) helped reveal relationships that were otherwise obscured by large intra-species variation in $\delta^{15}N$. Such an approach may therefore contribute to synthetically quantify the average trophic position of biomass of each size class of consumers across the size spectrum.

In this study, we examine the effects of three variables associated with bottom-up processes on lotic invertebrate density: system productivity, temperature and trophic position. Using an ataxonomic approach (organisms pooled by size class irrespective of their taxonomic affiliation), we first examine the relationships between invertebrate density and size and between trophic position of invertebrate biomass and size in 23 communities from rivers varying in productivity and temperature. Secondly, we examine the effect of productivity using N, P (nutrients limiting primary production in aquatic systems), and chlorophyll *a* (indicator of primary producers biomass), as well as the effect of temperature on the density of the ten size classes. We also look at the relationships between density and trophic position of invertebrate biomass within individual size classes of the size spectrum. Finally, we

examine the effects of all variables (size, trophic position, N, P, chlorophyll *a* and temperature) on lotic invertebrate density using a multiple regression approach over the complete range of size classes.

3.2. Methods

3.2.1. Study sites and water quality data

Invertebrates were sampled in August 2003 from 23 river sites located in 11 watersheds draining the St-Lawrence Lowlands in Québec, Canada (Fig. 3.1). Sampling stations were located in riffle sections. In particular, we sampled substrata composed of rocks of similar size in order to reduce the effect of the type of substratum sampled on invertebrate density (mean rock size (longest axis and the axis perpendicular to the longest axis) = 17.0 by 11.8 cm; based on a mean of 15 average-sized rocks measured at each study site (5 rocks x 3 subsites by study site). Watershed area ranged from 175 km² to 42 820 km². Watersheds were characterized by varying land use types and anthropogenic activities (see Anderson and Cabana 2005, 2006).

Sites were selected to reflect a gradient in productivity, and ranged from oligotrophic to eutrophic (Table 3.1). Concentrations of nitrogen (Total N (dissolved and particulate), mg/L), phosphorus (Total P (dissolved and particulate), mg/L), chlorophyll *a* (mg/m³; in water column), and temperature (°C) in river water were estimated for all study sites (except temperature which was available for 22 out of 23 sites) using water quality monitoring databases from the Ministère de l'Environnement du Québec (2004). These water quality monitoring sites were located near our study sites (< 1.5 km (57% of sites located < 500 m), except two monitoring sites located ~4 km and 10 km away respectively from our study sites, but which did not show any significant change in land use). Estimated values were based

on a five-year average ranging from august 1998 to august 2003 (five years prior to sampling). Available chlorophyll *a* values spanned over the summer period (May to October), whereas N, P, and temperature values ranged over the entire year. Measurements were taken, on average, once or twice per month for each study site (more details on data collection can be found in the water quality monitoring database of the Ministère de l'Environnement du Québec (2004)). We assume in this study that water column chlorophyll *a* is a relevant indicator of large river productivity. Several studies have found significant relationships between sestonic chlorophyll *a* levels and N and P concentrations in rivers (e.g., Basu and Pick 1996; Van Nieuwenhuyse and Jones 1996; Smith 2003) and thus suggest that water column chlorophyll *a* could be used as an indicator of the trophic level (~productivity level) of rivers.

3.2.2. Sampling and identification

Invertebrates were collected in August 2003 using Surber nets (0.1 m^2; 0.6 mm mesh size) and D-frame aquatic nets (1 mm mesh size). Four Surber replicates were taken at each site. Samples were kept in coolers and frozen within eight hours and then thawed for sorting and identification. Invertebrates caught with D-frame nets were sorted and identified to family or genus according to Merritt and Cummins (1996) and Thorp and Covich (1991). Invertebrates collected with Surber nets were sorted by size class by washing organisms through a series of 10 brass-frame laboratory sieves (mesh sizes: 0.5, 0.71, 0.85, 1, 1.41, 2, 2.83, 3.36, 4, and 8 mm), and identified to family. Invertebrates that fell through the 0.71 mm mesh size sieve but which were retained by the 0.5 mm mesh size sieve were kept in all analyses, despite the fact that the Surber net had a mesh size of 0.6 mm. This could have induced certain variability in the 0.5 mm size class results. However, a laboratory test using a smaller sieve (0.25 mm mesh size) showed that a large proportion of smaller sized invertebrates – which also fell through the 0.5 mm mesh size sieve – were

caught by the 0.6 mm-mesh Surber (personnal observations), suggesting that the invertebrate density of the 0.5 mesh-size sieve might not be as largely underestimated as initially expected. Invertebrates caught with Surber nets were used to calculate densities and trophic positions of the various size classes of the communities examined. Invertebrates collected using the D-frame nets were all primary consumers, which were used to calculate baseline $\delta^{15}N$ values for each study site in order to estimate trophic position of size classes (see section below).

Organisms collected with Surber nets were pooled by size class for isotopic analyses (irrespective of their taxonomic group). Two samples randomly drawn from the four surber samples collected on the field were analysed for each study site. Replicates showing too small amounts of material for isotopic analyses were pooled for some sites (replicates of the 0.5, 0.71 and 0.85 mm classes were combined for 15, 12, and 8 sites, respectively). Invertebrates collected using D-frame nets were pooled by genus or family. Invertebrates were used whole, except molluscs which were removed from their shell. Non-animal materials were removed from the samples prior to isotopic analyses. All samples were dried at 60 °C for at least 48 hours and ground into a homogenous powder. Isotopic analyses were performed at the University of New Brunswick with a Finnigan-Mat Delta Plus mass spectrometer. A total of 522 samples were analysed. Forty-three samples were analysed in duplicate and showed a mean standard deviation of 0.24‰. This slightly larger standard deviation observed in comparison with our previous isotopic studies (Anderson and Cabana 2005, 2007; s.d. = 0.17‰) might result from pooling organisms belonging to different taxonomic groups.

3.2.3. Trophic position estimates

Several past studies have reported large spatial variations in $\delta^{15}N$ values measured at the base of food webs and have associated them with land use change

(Cabana and Rasmussen 1996; Hebert and Wassenaar 2001; Anderson and Cabana 2005, 2006). To compare $\delta^{15}N$ values across sampling sites, we corrected the $\delta^{15}N$ values of the different size classes with the $\delta^{15}N$ values of baseline organisms. More precisely, we used the procedure detailed in Anderson and Cabana (2007) to select baseline organisms and estimate trophic position of size classes. Briefly, ubiquitous primary consumers (scrapers) with low $\delta^{15}N$ values were used as baseline indicators. In addition, we also included $\delta^{15}N$ values of hydropsychids (Trichoptera: Hydropsychidae) in the baseline $\delta^{15}N$ estimates because they were dominant in numerous sites and their exclusion would have lead to a smaller number of sites for which trophic position could have been estimated. Before computing baseline $\delta^{15}N$, we corrected Hydropsychidae $\delta^{15}N$ values toward Psephenidae (Coleoptera) $\delta^{15}N$ as shown in Anderson and Cabana (2007). The mean difference between hydropsychids and psephenids calculated using the dataset of Anderson and Cabana (2007), was of 1.42 ‰ (paired t-test, Bonferroni corrected; $p < 0.0001$). We thus used this value to correct Hydropsychidae $\delta^{15}N$ downwards toward Psephenidae $\delta^{15}N$. Last, $\delta^{15}N$ values of Ephemerellidae (*Drunella*), Heptageniidae (*Heptagenia* and *Stenonema*), and Hydropsychidae were all corrected towards Psephenidae $\delta^{15}N$, as shown in Anderson and Cabana (2007), and $\delta^{15}N$ values of these four families were averaged by site to yield baseline $\delta^{15}N$.

Using this baseline $\delta^{15}N$, we estimated the trophic position of size classes (biomass combining several consumers) following the equation:

$$\text{Trophic Position}_{\text{size class}} = ((\delta^{15}N_{\text{size class}} - \delta^{15}N_{\text{baseline}})/ 3.4) + 2 \qquad (1)$$

where $\delta^{15}N_{size\ class}$ is the $\delta^{15}N$ value of the size class for which the trophic position is estimated, $\delta^{15}N_{baseline}$ is the $\delta^{15}N$ value of the baseline organism, and 2 is the expected trophic position of the organism used to estimate baseline $\delta^{15}N$ (e.g., an herbivore).

3.2.4. Statistical analyses

Densities and trophic positions obtained for the two Surber replicates were averaged by site for each size class. Density was reported as number of individuals•m^{-2}. Relationships between density and size class (sieve size), and trophic position and size were examined using polynomial regression analyses (Zar 1999). Lower class limits were used as size class in all analyses. A covariance analysis (ANCOVA; Tabachnick and Fidell 2001) was conducted to further examine the relationship between trophic position and size across sites and to examine the combined effect of site and size. Linear regression analyses and a principal components analysis (Tabachnick and Fidell 2001) were also performed in order to examine relationships between density and trophic position within and among size classes.

In addition to trophic position, we tested the potential effect of productivity (Total N, total phosphorus P, and chlorophyll *a*) and temperature on density. Linear regression analyses were used to investigate the effect of variables related to productivity and temperature on the density of individual size classes and on total density (density of all size classes summed by site). Finally, multiple regressions analyses were used to determine the relative effect of size, trophic position, productivity and temperature on the density of all samples.

Statistical analyses were performed using SYSTAT (Version 8.00, SPSS Inc. 1998), SAS (Version 8.0, SAS Institute Inc. 1999), and Canoco (Version 4.5, Biometris 2002). In all cases, size and density were log-transformed (log_{10}) in order

to meet the assumptions of regression analysis. One unit was added to density prior to log transformation because of the presence of zeros (log density + 1). N, P and chlorophyll *a* were square-root transformed to meet regressions assumptions. These square-root transformations were chosen over log-transformation because they produced the skewness and kurtosis values nearest zero and the distribution nearest to normality (Tabachnick and Fidell 2001).

3.3. Results

3.3.1. Density-size relationships

Density significantly declined with size class (Fig. 3.2; $r^2 = 0.47$, $p < 0.0001$). The relationship was best explained by a second order polynomial regression. The overall pattern was hump-back shaped, with highest densities measured at the 1 mm sieve size class (mean density of 978 individuals$\cdot m^{-2}$; mean length corresponding to ~4 mm (based on the relationship between sieve size and invertebrate body length measured for two of our study sites – one oligotrophic and one eutrophic site)). Density within individual size classes varied over close to two orders of magnitude among sites (Fig. 3.2), with most of this variation attributable to sites (Anova performed on each size class and using site as a factor: r^2 of size classes = 0.62 to 0.82 ($p < 0.05$), except for the 8 mm size class which showed no significant difference in density among sites ($p > 0.05$), probably because of the presence of several zeros).

3.3.2. Trophic position-size relationships

Mean trophic position of biomass increased significantly with size (Fig. 3.3; $r^2 = 0.96$, $p < 0.005$). The average increase between the smallest and the largest size class corresponded to 0.41 trophic levels. A covariance analysis using size and study sites as factors showed that this pattern of increase was significantly different among

the 23 study sites (interaction of site and $\log_{10}$ size on trophic position: $F = 3.78$, $df = 22, 198$, $p < 0.0001$). Indeed, 14 sites showed significant increases in trophic position with size ($p < 0.05$; slopes (linear) ranging from 0.54 to 6.78), whereas the 9 remaining sites showed no significant trends ($p > 0.05$). A large variability in trophic position was also observed within individual size classes, standard deviations spanning up to 0.42 trophic levels. This variability was high for all ten size classes and was mostly attributable to site effects (Anova using site as a factor: r^2 of individual size classes ranging from 0.70 to 0.96 ($p < 0.05$)), suggesting spatial heterogeneity in the trophic position of organisms belonging to any given size class.

3.3.3. Factors affecting density

3.3.3.1. Productivity and temperature

Mean concentrations of N, P and chlorophyll *a* were used as potential indicators of productivity. All three variables varied greatly among study sites and reflected oligotrophic to eutrophic systems (Table 3.1). Mean temperatures also varied among sites and ranged from 6 to 14.7°C (Table 3.1). Temperature was slightly, but significantly correlated with chlorophyll *a* (Pearson correlation: $r = 0.46$, $p < 0.05$) and P ($r = 0.45$, $p < 0.05$). Chlorophyll *a* concentrations were also significantly correlated with N ($r = 0.74$, $p < 0.0001$, $n = 23$) and P concentrations ($r = 0.79$, $p < 0.0001$, $n = 22$ (excluding one site showing abnormally high P values associated with raw sewage discharges (pers. Observation)).

Density of each of the ten size classes taken individually was not significantly correlated with N and P concentrations ($p > 0.05$) across study sites. However, density of the 3.36 and 8 mm size classes increased significantly with higher chlorophyll *a* concentrations (3.36 mm: $r^2 = 0.20$, $p < 0.05$; 8 mm: $r^2 = 0.25$, $p < 0.05$). The density of four other size classes (0.85, 1.41, 2, and 2.83 mm) also tended to increase with higher chlorophyll *a* concentrations ($p < 0.10$). A small trend towards higher densities in more productive systems was also found when the densities of the

ten size classes were summed by site (n = 23). Sites exhibiting higher chlorophyll *a* concentrations tended to show higher total densities (linear regression: $r^2 = 0.15$, $p = 0.07$). Neither density of the ten size classes taken individually nor total density (sum of the 10 size classes) were affected by average annual water temperature ($p > 0.05$). Moreover, total density was not significantly influenced by N or P ($p > 0.05$).

3.3.3.2. Trophic position

No significant relationship was found between density and trophic position for any of the ten size classes examined (linear regression; $p > 0.05$). The 1 mm size class, however, showed a small trend towards a decrease in density with increasing trophic position ($r^2 = 0.14$, $p = 0.07$). When examining the relationship between density and trophic position simultaneously for all ten size classes using a Principal components analysis, we found that densities were not diametrically opposed to trophic positions, as initially expected (Fig. 3.4). However, trophic position estimates of the ten size classes were generally correlated with one another (arrows in the same direction, Fig. 3.4). Densities of the ten size classes were also correlated with one another.

3.3.3.3. Multiple regressions

We examined the combined effect of size, trophic position, productivity (N, P, and chlorophyll *a*), and temperature on density with a multiple regression analysis (forward stepwise regression analysis using $p = 0.05$ to accept or reject variables) using all samples (n = 230). Since the initial relationship between density and log size was best explained by a second order polynomial regression, we also added the term $[\log_{10} \text{size}]^2$ in the multiple regression. We found that trophic position, P and temperature did not contribute significantly to changes in density ($p > 0.05$), nor did $\log_{10}$ size. $[\text{Log}_{10} \text{size}]^2$, chlorophyll *a* and N significantly affected densities ($p < 0.05$). Using these three variables, we obtained the following equation:

$$\text{Log density} = 2.25\ (\text{constant}) - 2.01\ [\text{Log}_{10}\ \text{size}]^2 + 0.358\ \text{chlorophyll}\ a^{0.5} - 0.579\ N^{0.5} \qquad (2)$$

The multiple r^2 of this relationship was 0.56 ($p < 0.0001$). Size ($[\log_{10}$ size$]^2$) accounted for 47% of the variation, whereas chlorophyll *a* and N accounted for an additional 5 and 4%, respectively.

3.4. Discussion

3.4.1. Density-size relationships

Size explained 47% of the variation in density of the lotic invertebrate communities examined in the current study. Previous studies of mammalian population density found that size was an important predictor of mammal density. Peters and Raelson (1984) found that size (body mass) explained 63% of mammal density (including herbivores, carnivores and omnivores). Similarly, Damuth (1981) showed that a large proportion of mammal density was correlated with mammal body mass ($r = -0.86$). In a survey on the effect of body size on the density of various animals (including mammals, birds, vertebrate poikilotherms and invertebrates), Peters and Wassenberg (1983) found that 81% of variability in density ($\log_{10}$) of animals was explained by size ($\log_{10}$ body mass).

In aquatic ecosystems, Damuth (1987) and Cyr et al. (1997a) found strong negative relationships between density and body size of aquatic organisms ($r^2 = 0.81$ and 0.92, respectively). These proportions are greater than the one observed in the current study. This difference can be attributable to the range of body size used. For instance, body sizes examined in Cyr et al. (1997a) spanned from phytoplankton to fish. In the current study, we only examined benthic invertebrates (larger than phytoplankton but smaller than fish). Studies examining a more restricted range of

body sizes obtained results similar to ours. Peters and Wassenberg (1983) found that aquatic invertebrate body size explained 54% of variation in density. Likewise, Schmid et al. (2000) and Solimini et al. (2001) found that body mass explained 46 to 51% of the abundance of benthic invertebrates in streams and rivers.

In the present study, high variability was found among densities of a given size class. Such variability was observed in other studies such as Brown et al. (2004), who have observed variations of two orders of magnitude in population densities of species of any given size. They attributed part of this large variability to changes in trophic position (change in diet from herbivore to carnivore) and in resource supplies (e.g., productivity). We discuss these factors in the next paragraphs.

3.4.2. Trophic position-size relationships

Mean trophic position significantly increased with size. This increase was relatively modest (slightly lower than 0.5 trophic level) for the size range examined (sieve sizes corresponding to mean body lengths of ~2 mm to 25 mm). Several studies have observed significant increases in $\delta^{15}N$ values with body size of individual invertebrate and fish species (Branstrator et al. 2000; Badalamenti et al. 2002; Jennings et al. 2002; Deudero et al. 2004), as well as of entire zooplanktonic (Fry and Quinones 1994; Montoya et al. 2002) and benthic communities (France et al. 1998; Jennings et al. 2002). The mean increase in trophic position found by France et al. (1998) between herbivorous (snails) and predatory invertebrates (Dragonflies) collected in lakes (~1 trophic level) was much larger than ours. Our smaller overall increase in trophic position with size could be attributable to our ataxonomic approach, which combined predatory and non predatory organisms in the same size classes. For instance, large primary consumers such as shredders (e.g., Pteronarcydae (Plecoptera)) were sometimes pooled with large predatory consumers (e.g., Perlidae (Plecoptera) or Corydalidae (Megaloptera)) for isotopic analyses. Additionally, the

variability in the direction of slopes from one site to another (trophic position not always increasing with size across sites) may have dampened the overall increase in trophic position with size. Other studies examining changes in $\delta^{15}N$ of aquatic communities with size using ataxonomic data have generally found small changes in trophic position with size. For instance, Jennings et al. (2002) found an increase of ~0.5 trophic levels for invertebrates with body mass ranging from 0.06 to 32 g. Similarly, Fry and Quinones (1994) observed a change of 0.5 to 0.75 trophic levels across seven zooplankton size fractions ranging from 0.064 to 8 mm. These small increases have been attributed to overlap in trophic position among the size classes studied and support our findings.

Even though the observed increase in trophic position with size was small, our results suggest that the proportion of predatory and/or omnivorous organisms increase with body size. Increasing consumption of animal matter with size has been observed for several species. For instance, Fuller and Mackay (1980) have observed greater consumption of animal matter by large collectors (hydropsychids) relative to smaller ones. Similarly, studies on the feeding behaviour of predatory stoneflies (Fuller and Stewart 1979; Allan 1982; Allan et al. 1987) have found that larger individuals consumed greater amounts of animal matter and larger prey than smaller ones. Overall, our findings are consistent with Wilson (1975) and Cohen et al. (1993). They proposed that, as size of organisms increase, so does their potential to ingest other animals, including larger and more carnivorous species.

Lastly, we found that trophic position varied greatly within size classes. This observation suggests that there is great variability in the trophic composition of size classes across study sites (heterogeneity in food web structure).

3.4.3. Factors affecting density

3.4.3.1. Productivity and temperature

Significant increases in densities in two of the largest size classes were associated with increases in productivity (chlorophyll *a* in particular). Density of four other size classes and total density (sum of all size classes) also tended to increase with chlorophyll *a* concentrations. Several studies have found positive effects of productivity on aquatic invertebrate densities. For instance, Hart and Robinson (1990) found that grazers became more abundant in P-enriched treatments. Similarly, Perfin and Richardson (1997) found higher densities of midges and mayflies in treatments receiving greater additions of N or N and P. Sardá et al. (1996) also observed greater invertebrate abundances in fertilized creeks compared to control ones. Such studies proposed that the addition of nutrients limiting growth of primary producers in a given system will yield greater amounts of food supply (or energy) that will, in turn, support greater densities of consumers. Hence, higher productivity at the base of the food web should be associated with higher productivity in the higher echelons of that same food web. This theory has been further supported by field studies which have found higher densities of invertebrates in aquatic systems affected by important nutrient runoff (Corkum 1990; Harding et al. 1999; Manel et al. 2000). Our results are concordant with these studies and showed higher densities in communities inhabiting more productive river sites (measured as chlorophyll *a*). The absence of relationship between density and N or P (despite the significant relationship with chlorophyll *a*), could be explained by the fact that N and P concentrations are tightly associated with human activities on our watersheds (see Anderson and Cabana 2006) and therefore may be partly associated with human pollution and not just productivity (see multiple regressions section below). Moreover, N and P may be depleted in the growing season (assimilated by primary producers), thus the annual values used might be poor indicators of system productivity.

Previous studies have also analysed the effect of productivity on different size classes. Cyr et al. (1997b) examined the effects of various environmental conditions on the density-size relationship in aquatic communities (ranging from phytoplankton to fish). They predicted that density would increase with productivity, but that the density of smaller organisms would increase more rapidly than the density of larger ones. They based their hypothesis on the fact that energy transfer is likely less efficient with increasing trophic level, leading to slower increases in density of large organisms. Their results were concordant with their prediction. In the current study, we did not find a greater increase in the density of small organisms compared to larger ones. Instead, we found significant effects of productivity on the density of two of the largest size classes. However, the size scale used by Cyr et al. (1997b) was much broader than the one used in the current study. Perhaps our size interval was not broad enough to reveal trends such as those found by Cyr et al. Finally, Bourassa and Morin (1995) have also examined the effect of productivity on aquatic invertebrate abundance. They found a significant increase in invertebrate abundance with increasing total phosphorus concentration. More precisely, they observed a greater increase in the abundance of large organisms in richer sites compared to smaller ones, which is concordant with our findings.

Warmer temperatures are known to increase growth rate, reduce development time and increase overall biological activity of organisms (Cossins and Bowler 1987; Gillooly et al. 2001; Brown et al. 2004). In addition, warmer temperatures can improve food quality and quantity in aquatic systems by enhancing periphyton and microbial growth (Cummins and Klug 1979; Sweeney 1984), which in turn support larger populations of consumers. Correspondingly, temperature was significantly correlated with chlorophyll *a* across our study sites, suggesting that it is a potential index of site productivity (note however, that this relationship could be partly caused by the fact that the highly agricultural watersheds (potentially more productive) were more southern than the forested ones). Hence, we expected higher temperatures to be

associated with higher aquatic invertebrate densities. Previous field experiments found that annual aquatic invertebrate production increased with mean annual water temperature (Plante and Downing 1989; Morin and Bourassa 1992). Several studies examining the effects of cooling water effluents from power stations on aquatic biota have also found increases in the abundance of some species below the heated effluents (Hellawell 1986 and references therein). Although mean annual temperature ranged from 6 to 15 °C across our study sites, we did not observe any significant effect of temperature on invertebrate density (neither for total density nor density for individual size classes). The effect of temperature could have been obscured by other factors such as predation, habitat structure or disturbance, which potentially vary greatly among our study sites. Furthermore, invertebrate density was measured only once during the year (august). To better assess the effect of annual temperatures on invertebrate densities, it might be recommended to use annual mean densities (e.g., several sampling dates throughout the year).

In general, our findings differ from what was initially expected. They do not agree with the hypotheses that 1) the density of small organisms, which have faster growth rates than larger ones (Hennemann 1983; Gillooly et al. 2001; Savage et al. 2004), should increase faster in productive and warmer sites relative to larger organisms and that 2) energy transfer is less efficient for higher trophic levels (larger organisms), yielding slower increases in density compared to smaller organisms (Cyr et al. 1997b and references therein). They rather suggest that productivity raises the density of larger organisms slightly more than the density of small organisms. This finding can be explained by different hypotheses. First, productive systems provide greater food supplies which in turn might enhance the growth of organisms, leading to larger average individuals (at any echelon of the food web). Secondly, because of top-down processes, higher productivity might lead to higher densities of top consumers (larger organisms), but not of smaller organisms located lower in the food web, which are controlled by their predators (Fretwell 1977; Arruda 1979; Oksanen et

al. 1981). The number of trophic levels in the systems we examined might favour an increase in density of larger (potentially more predacious) invertebrates, but a stabilization of the density of smaller organisms.

3.4.3.2. Trophic position

Our initial hypothesis was that trophic position would be a good predictor of density. More precisely, we suggested that higher trophic positions would lead to lower densities. We based this prediction on the energetic efficiency hypothesis (e.g., Lindeman 1942; Kerr and Dickie 2001), which suggest that predators of a given size should be less abundant than herbivores of the same size because of energetic inefficiencies in the transformation of energy with increasing trophic level. In a recent study examining pelagic food web attributes, Cohen et al. (2003) concluded that trophic height (similar to our concept of trophic position) explained part of the variation in numerical abundance but much less than did average body size. However, variation in trophic height was generally associated with changes in size and they did not examine the effect of trophic position within given size classes. In the present study, we found no relationship between density and trophic position for the entire community nor within size classes. Perhaps the effect of trophic position was obscured by other factors such as predation or pollution (see below – multiple regression section). Also, the use of a single fractionation value (3.4‰) may have induced some variability in our trophic position estimates across sites. Indeed, several studies question the use of a single fractionation value and have found variable fractionation in ^{15}N among functional feeding groups and with changes in diet quality (Vander Zanden and Rasmussen 2001; McCutchan et al. 2003; Jardine et al. 2005). This means that our trophic position estimates could partially be affected by differential fractionation among invertebrate groups and across sites. However, in a previous study (Anderson and Cabana 2007), we found that trophic position estimated using a single fractionation value (3.4‰) still reflected general feeding patterns of organisms (distinguishing between herbivores and carnivores).

Consequently, the use of a single fractionation value might have introduced some variability in our trophic position estimates but is likely not responsible for the lack of relationship between density and trophic position. Lastly, the lack of relationship between density and trophic position could be attributable in part to the fact that invertebrate density and trophic position were measured only once during the year (August). The use of annual mean densities and trophic positions (several sampling dates throughout the year) in future studies could yield further insights on how year-round trophic position and densities are correlated with one another.

Trophic positions of the ten size classes were generally correlated across sites, suggesting that organisms of any size class in a given community share similar trophic positions (high or low). Hence, when small organisms exhibited higher trophic positions (compared to other study sites), so did medium- and large-sized organisms. This observation is potentially explained by the fact that small organisms with high trophic positions are assimilated by larger organisms which then also show higher trophic positions. This finding suggests that there is strong trophic connectivity among size classes in the studied food webs (e.g., no size class seems disconnected from the food web). However, the fact that organisms were pooled by size class (irrespective of their functional feeding group or taxa) potentially has averaged trophic positions and could be responsible for this apparent connectivity. It is also possible that the selected baseline organism showed lower or higher $\delta^{15}N$ values than other primary consumers, yielding a shift in trophic position for the entire food web. However, we previously showed that primary consumers (including potential baseline organisms) showed consistent trophic position ($\delta^{15}N$) across sites (Anderson and Cabana 2007). It is therefore unlikely that the selected baseline organisms accounted for such shifts.

Densities of different size classes were also correlated with each other. Sites showing high densities of small organisms also tended to show elevated densities of larger organisms. This observation suggests that systems that can support higher densities of small organisms can also support greater densities of larger organisms because 1) more energy at the base of the food web can support larger densities of herbivores, whether they are large or small and/or 2) greater densities of prey (small organisms) can support greater densities of predators (generally larger organisms). The fact that densities are correlated also suggests that there are no strong overwhelming top-down effects over the size range that we considered. Indeed, strong top-down effects would have generated discontinuities in the density-size distribution (series of peaks and gaps; Carpenter and Kitchell 1993), which would have been represented by opposed densities of certain size classes in the principal components analysis. Furthermore, top-down effects should have resulted in an inverse relationship between densities of small organisms and trophic positions of large organisms (e.g., higher trophic positions of larger organisms (higher proportion of predators) correlated with lower densities of smaller size classes (prey being fed on)). Previous studies have observed top-down effects among organisms corresponding to the size interval studied (e.g., dragonflies reducing chironomid densities; Benke 1978; Power 1990; Power et al. 1992). Hence, we expected to find inverse relationships between densities of small and large organisms, as well as between density of small organisms and trophic position of large organisms. The lack of apparent top-down effects may be due to our ataxonomic approach (especially if predators are specialists and do not systematically feed on any organisms found in a given size class) and to the combination of several sites not necessarily showing systematic top-down effects among the same size classes.

3.4.3.3. Multiple regressions

The inclusion of chlorophyll *a* and nitrogen into the size-density relationship slightly improved our prediction of total invertebrate density. The effect of size ([log

size]^2) on density, however, was much greater than the effect of chlorophyll *a* and N. This is not surprising since density was well correlated with size (Fig. 3.2). The sign of the constants indicates that density decreases with size, but increases with chlorophyll *a*. The multiple regression equation also suggests that density decreases with higher N concentrations. This last observation differs from what was expected. Indeed, higher N concentrations are generally associated with greater productivity and hence greater invertebrate densities. One explanation for this discrepancy could be that N is highly correlated with human activities on the studied watersheds (Anderson and Cabana 2006), and might therefore represent an index of human disturbance rather than of productivity (e.g., decreases density instead of increasing it). Previous studies have found lower invertebrate densities in sites affected by urban or industrial runoff (Mayack and Waterhouse 1983; Garie and McIntosh 1986; Pelletier and St-Onge 1998), and by agricultural runoff (Dewey 1986; Pelletier and St-Onge 1998), two activities that are associated with high N runoff in our study sites. In both cases, reduction in invertebrate densities was attributed to the presence of toxics (industrial wastes or pesticides). A second explanation could be that high nitrogen concentrations (ammonia in particular) can be toxic to aquatic life (Hellawell 1986; Ministère du Développement durable, de l'Environnement et des Parcs 2007), and could therefore reduce densities of intolerant species. Overall, these previous studies support our contention that certain human activities might lower aquatic invertebrate densities. Cyr et al. (1997b), who found that lakes characterised by large human population densities showed lower densities of small organisms (~invertebrates), also further support this hypothesis.

Overall, size explained a good proportion of the variation in density throughout the size range examined, whereas trophic position, productivity, and temperature did not explain a large fraction of this variation. In addition, these latter factors did not explain much of the variation in density within size classes. Other

factors such as predation, habitat structure and disturbance might affect aquatic invertebrate densities. First, top-down processes can alter invertebrate density. Several studies have demonstrated the importance of predation on the abundance of aquatic organisms. For example, Crawford et al. (2006) found that predation by crayfish lowered invertebrate abundance in streams. Similarly, other studies have observed lower densities of invertebrates when invertebrate-feeding fish showed higher densities (Crowder and Cooper 1982; Bowlby and Roff 1986; Power 1990; Diehl 1992). Moreover, fish predation can also modify invertebrate size structure, shifting benthos size towards smaller organisms (Crowder and Cooper 1982; Blumenshine et al. 2000; Diehl 1992). Habitat structure and escape from predation can also affect densities. By hiding or adopting particular strategies (e.g., armored organisms), organisms can maintain higher densities than predicted (Power et al. 1992; Wootton et al. 1996). For instance, Crowder and Cooper (1982) and Diehl (1992) found that habitat complexity constituted a refuge from predation and helped support higher invertebrate densities. Crowder and Cooper (1982) also found that fish at high macrophyte density (high refuge) ate fewer but larger prey, affecting the size distribution of the invertebrate community. In the present study, predation by fish and habitat structure might have affected both invertebrate densities of individual size classes and invertebrate densities of entire communities. The inclusion of both variables in future studies might help to explain a larger proportion of the observed variation in density.

Lastly, disturbance and pollution could also have contributed to changes in densities observed within size classes in the present study. Numerous laboratory and field studies have shown how pollutants altered aquatic invertebrate communities and reduced invertebrate abundances (e.g., Kiffney 1996; Maret et al. 2003; Kövecses et al. 2005). In particular, a review published by Ford (1989) showed that aquatic invertebrate densities often decreased with increasing chemical stress. However, one conclusion of this review was that tolerant species often replace less tolerant ones and

dominate the system, leading to an increase in pollution-tolerant species densities (and thus sometimes of the whole community). Moreover, polluted sites may favour a diminution of large invertebrate predators (e.g., Perlidae (Plecoptera) and Corydalidae (Megaloptera)), which are generally more sensitive than smaller, more tolerant species such as chironomids or oligochaetes (Resh et al. 1996; Pelletier and St-Onge 1998; Voshell 2002). This potentially generates a shift in the size spectra towards smaller organisms, affecting size distribution of invertebrates.

3.5. Conclusion

In conclusion, size explained almost half (47%) of the changes found in density throughout study sites. Productivity also explained a fraction of changes in total invertebrate density. However, large variation in density was found within individual size classes and none of the analysed variables explained a substantial amount of this variation. Our predictions were mostly based on the effects of bottom-up processes (available energy and energy transfer up the food web). The lack of correlation between density and the variables used, combined with the large variation in density found within size classes, suggest that other factors such as top-down processes or disturbance may have a greater influence on lotic invertebrate density.

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Table 3.1. Total N, Total P, chlorophyll *a* (water column) and water temperature values for the 23 study sites. *n* represents the number of samples taken for each of the 23 study sites (range) for each variable. More details are presented in the methods section.

Variable	**Mean**	**Min**	**Max**	**SD**	***n***
Chlorophyll *a* (mg/m^3)	4.96	0.66	16.92	4.00	15-38
Nitrogen (mg/l)	0.91	0.22	2.33	0.62	17-64
Phosphorus (mg/l)	0.056	0.009	0.231	0.049	17-63
Temperature (°C)	10.3	6.0	14.7	1.9	38-61

3.8. Figure Captions

Figure 3.1. Stations sampled during summer 2003.

Figure 3.2. Relationship between $\log_{10}$ density and $\log_{10}$ sieve size ($r^2 = 0.47$, $p < 0.0001$). The equation for the regression curve is: $\log_{10}$ (density + 1) = 2.65 - 0.15 ($\log_{10}$ sieve size) - 1.82 ($\log_{10}$ sieve size)^2.

Figure 3.3. Relationship between mean trophic position and $\log_{10}$ sieve size ($r^2 = 0.96$, $p < 0.005$). The regression equation is : Trophic position = 2.08 + 0.13 ($\log_{10}$ sieve size) + 0.37 ($\log_{10}$ sieve size)^2.

Figure 3.4. Principal components analysis of density (D) and trophic position (TP) for the ten studied size classes. Size classes are: 1 (0.5 mm), 2 (0.71 mm), 3 (0.85 mm), 4 (1 mm), 5 (1.41 mm), 6 (2 mm), 7 (2,83 mm), 8 (3,36 mm), 9 (4 mm), and 10 (8 mm). The first and second axes account for 48% and 23% of the variability in the dataset, respectively.

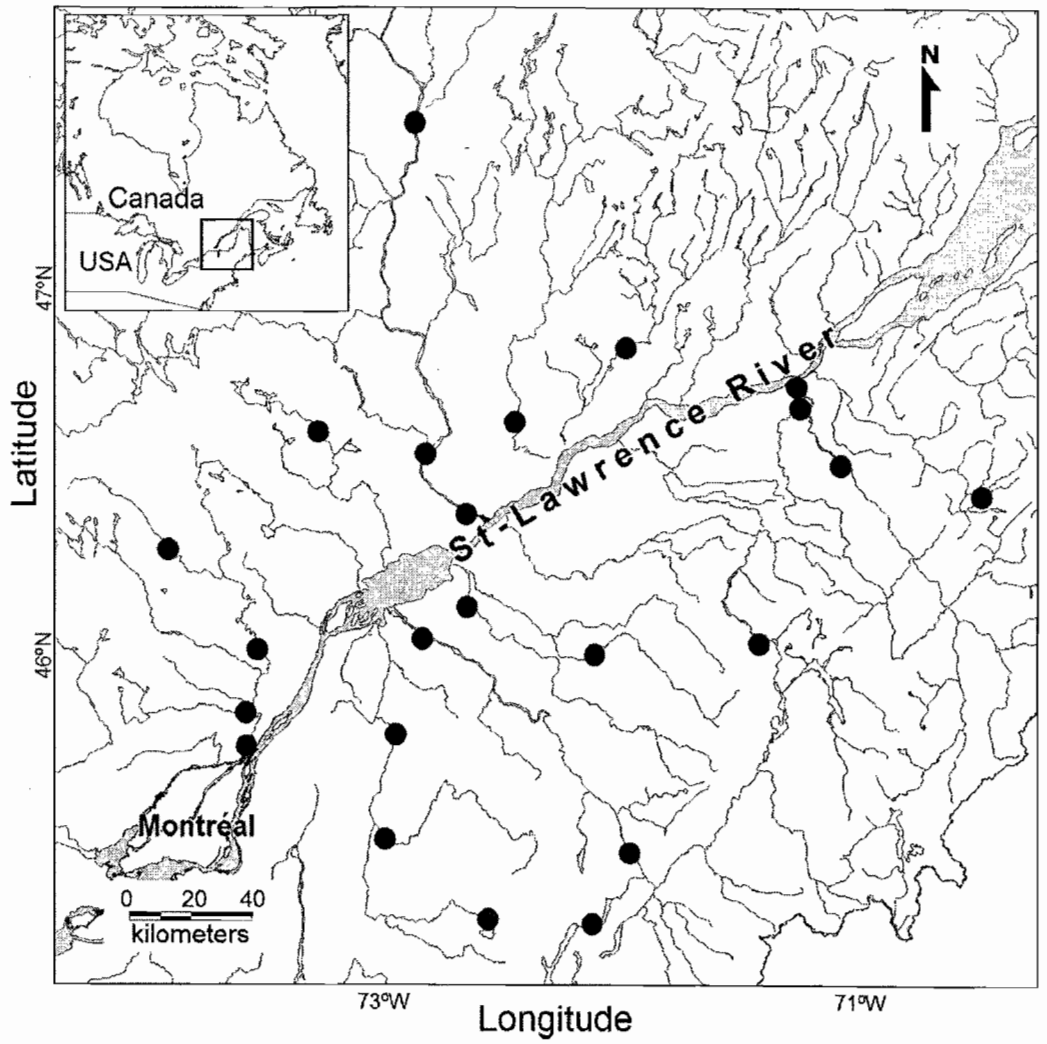
Canada
USA
N
St-Lawrence River
Montréal
0 20 40
kilometers
47°N
46°N
73°W
71°W
Latitude
Longitude

Figure 3.1.

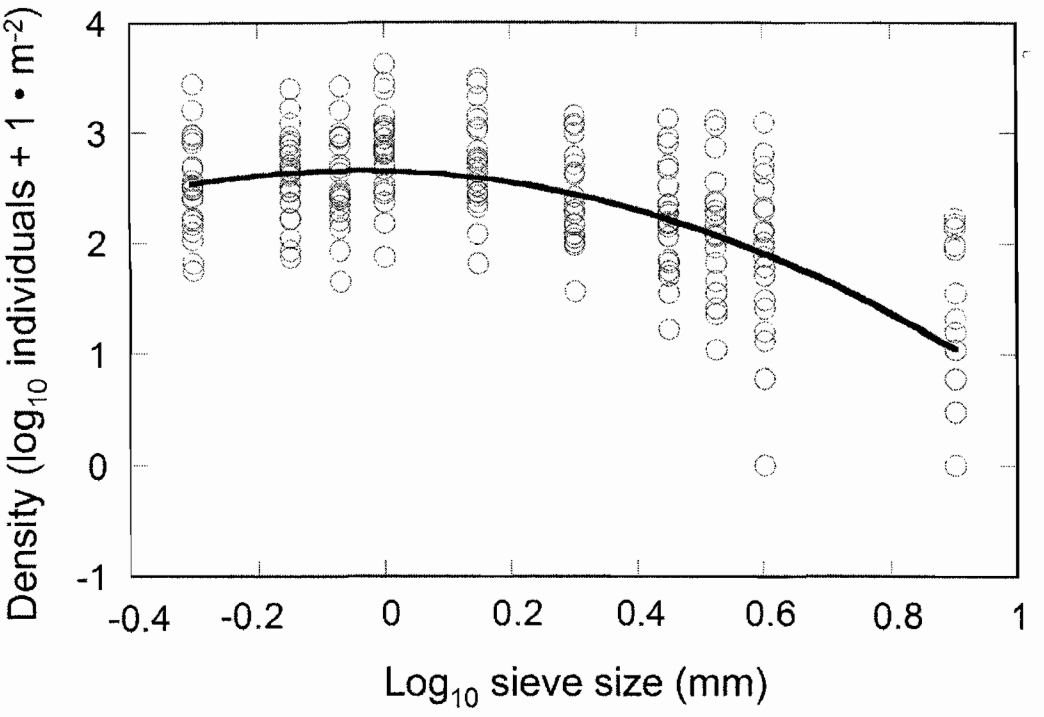
Density (log_{10} individuals + 1 • m^{-2})
4
3
2
1
0
-1
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Log_{10} sieve size (mm)

Figure 3.2.

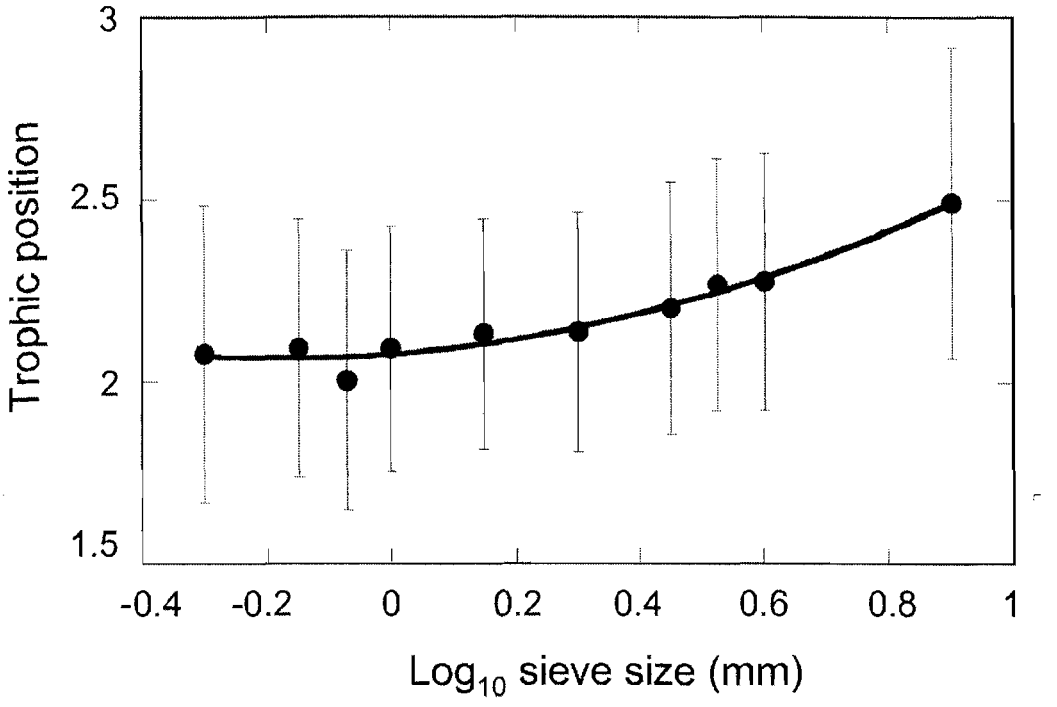
Trophic position
3
2.5
2
1.5
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Log10 sieve size (mm)

Figure 3.3.

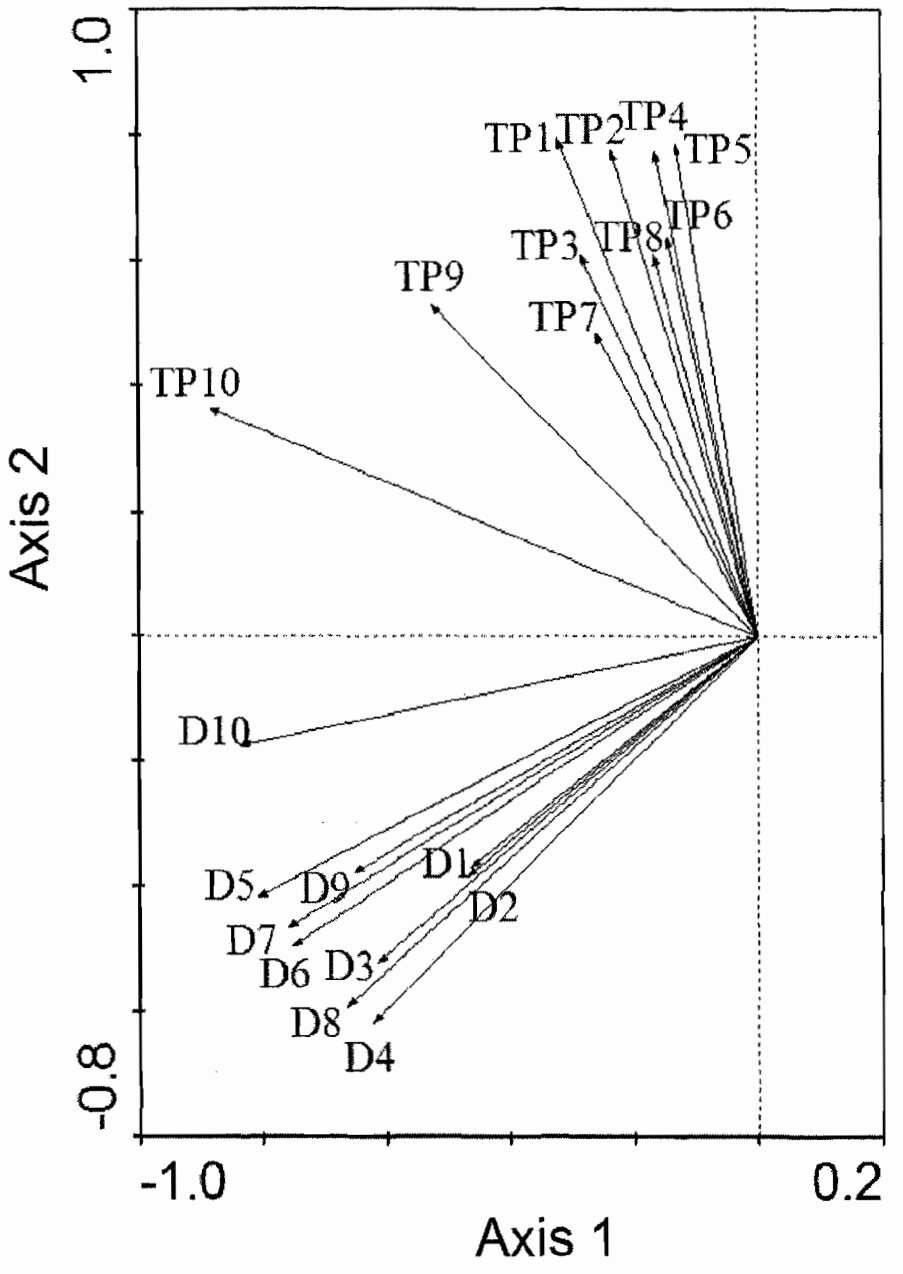
1.0
-0.8
Axis 2
-1.0
0.2
Axis 1
TP1
TP2
TP4
TP5
TP6
TP8
TP3
TP9
TP7
TP10
D10
D5
D9
D1
D2
D7
D6
D3
D8
D4

Figure 3.4.

CHAPITRE 4

ALTÉRATION DE LA STRUCTURE DES RÉSEAUX TROPHIQUES LOTIQUES PAR LES ACTIVITÉS HUMAINES: UNE APPROCHE ISOTOPIQUE

ALTERATION OF LOTIC FOOD WEB STRUCTURE BY HUMAN ACTIVITIES: EVIDENCE FROM NITROGEN ISOTOPES

Résumé

De nombreux chercheurs ont tenté d'élucider les facteurs régulant la longueur des chaînes alimentaires dans la nature. Deux facteurs pouvant potentiellement expliquer la variation dans la longueur des chaînes sont la productivité et les perturbations. On s'attend à ce que la productivité augmente la longueur des chaînes alimentaires, mais, à l'inverse, que les perturbations réduisent cette dernière. Les activités humaines sont à la fois une source de productivité et de perturbation. Conséquemment, nous avons voulu examiner l'impact des activités humaines sur les réseaux trophiques lotiques à l'aide des isotopes de l'azote ($\delta^{15}N$). En particulier, nous avons utilisé 1) la position trophique des petits poissons et 2) les pentes $\delta^{15}N$ - taille de la communauté d'invertébrés en tant que variables reflétant la longueur de la chaîne alimentaire. Les positions trophiques et les pentes variaient grandement entre les sites d'étude (position trophique = 0,4 à 1,9; Pentes = -1 à +2,8), suggérant une hétérogénéité dans la structure des réseaux trophiques. La position trophique des poissons n'était pas affectée par la productivité (chlorophylle *a*) ou les perturbations (industries dans le bassin versant). Cependant, les pentes $\delta^{15}N$-taille augmentaient significativement en fonction de la productivité et diminuaient significativement avec l'augmentation des perturbations. Les pentes tendaient également à être plus fortes lorsque la proportion de prédateurs dans la communauté était plus élevée en fonction de la taille (pentes pourcentage prédateurs-taille plus fortes). Ces résultats suggèrent que, lorsque la productivité est élevée et que les perturbations sont faibles, le $\delta^{15}N$ augmente rapidement avec la taille, contribuant ainsi à de plus longues chaînes alimentaires. Ils suggèrent aussi que les relations $\delta^{15}N$-taille des communautés d'invertébrés peuvent être utilisées comme indicateurs de l'altération des réseaux trophiques lotiques par les activités humaines.

Abstract

Numerous researchers have sought to identify the factors regulating food chain length in nature. Two factors expected to explain variation in food chain length are resource availability (productivity) and disturbance. Productivity is expected to enhance food chain length whereas disturbance is expected to reduce it. Human activities can be both a source of disturbance and productivity. We examined the impact of anthropogenic activities on lotic food webs using nitrogen isotopes ($\delta^{15}N$). We used 1) trophic position of small fish and 2) slopes of $\delta^{15}N$-size class relationships in the invertebrate community as variables related to food chain length. Trophic positions and slopes varied greatly among study sites (Trophic position = 0.4 to 1.9; Slopes = -1 to +2.8) suggesting heterogeneity in food web structure. Trophic position of fish was not affected by productivity (chlorophyll *a*) or disturbance (industries on the watershed). However, $\delta^{15}N$-size slopes significantly increased with productivity and decreased with disturbance. Slopes also tended to be greater when the proportion of predators found in the community increased in larger size classes. These results suggest that when productivity is high and disturbance is low, $\delta^{15}N$ increases faster with size, thus contributing to longer food chains. They also suggest that $\delta^{15}N$-size relationships of invertebrate communities may be used as indicators of food web structure alteration by human activities.

Keywords: Community, Fish, Invertebrate, Lotic, Perturbation, Productivity, Nitrogen isotopes, Trophic position.

4.1. Introduction

In past decades, numerous researchers have sought to identify the factors regulating food chain length in aquatic and terrestrial ecosystems. Two of the most widely discussed factors are resource availability (productivity) and disturbance. The resource availability hypothesis suggests that there will be more trophic levels (longer food chains) in systems that are more productive (Fretwell 1977; Oksanen et al. 1981), because higher productivity at the base of the food web can support larger populations of any consumers (primary, secondary, etc.). However, recent reviews have questioned this approach and proposed that high levels of productivity can create instability which decreases food chain length rather than increasing it (Morin and Lawler 1995; Post 2002a). Similarly, contradictory results have been found concerning the disturbance hypothesis. Early studies suggested that food chain length should decline with increased disturbance or environmental stress (Odum 1985; Menge and Sutherland 1987). For instance, Jenkins et al. (1992) observed shorter food chains in microcosms after a disturbance event (low rainfall). Likewise, Locke (1996) found that acidified (stressed) lakes generally showed lower food chain lengths than less acidified ones. Conversely, Power et al. (1996) and Wootton et al. (1996) observed that frequent floods (a disturbance) helped maintain longer food chains in Californian river systems. They found that the absence of floods favoured the development of large predator-resistant primary consumers, which short-circuited the energy flow and prevented it from going up the food chain.

Human activities can influence food chain length in aquatic ecosystems by affecting resource availability (release of large amounts of nutrients) and modifying disturbance regimes (translocation of contaminants, flooding regimes, etc.). For instance, high concentrations of anthropogenic nutrients (nitrogen, phosphorus) in aquatic systems could increase food chain length by inducing greater primary

productivity, which would subsequently support larger populations and diversities of higher consumers. Conversely, excessive amounts of nutrients could be toxic to aquatic life and reduce food chain length (hence becoming a disturbance). Highly productive systems (eutrophic) might also be characterized by oxygen deficiency, which affects several insects (Wiederholm 1984). Additionally, highly productive systems have been found to be less stable (Jenkins et al. 1992; Morin and Lawler 1995) and might therefore show shorter food chains than systems with intermediate-productivity levels. Most field studies have found lower species richness and simplified food webs in nutrient rich (agricultural) systems (Dance and Hynes 1980; Delong et Brusven 1998; Harding et al. 1998, Harding et al. 1999), supporting the argument that more productive systems should show reduced food chain length. Overall, food chain length might exhibit a humped relationship with productivity, food chain length being short when productivity is low (lack of energy), longer at moderate levels, and short again in highly productive systems. Such a relationship has been found by Persson et al. (1992) in lakes. Using chlorophyll *a* as a productivity index, they found that proportions of piscivorous fish were low in weakly and highly productive lakes, and highest in lakes with intermediate productivity levels. The presence or absence of piscivorous fish, which constitute the top predator in these lakes, suggest lengthening or shortening of the food chain. Contaminants released by industrial activities on the watershed (heavy metals, PCBs, etc.) could also affect food chain length. Several studies found lower species richness and simplified food webs in systems polluted by industrial contaminants (Ford 1989; Sibley et al. 2000; Sherwood et al. 2002). The disappearance of numerous species in the food web, in particular of large predators that are pollutant-sensitive (Resh et al. 1996), should yield shorter food chains in systems impacted by industrial activities.

Despite the increasing number of studies seeking to identify determinants of food chain length in aquatic systems, most patterns have remained unclear or contradictory. Additionally, previous food chain studies have either been limited to

simple food web descriptions using discrete trophic levels, which underestimated omnivory (Oksanen et al. 1981; Persson et al. 1992; Abrams 1993), or have necessitated intensive sampling and identifying efforts in order to properly evaluate food web structure (e.g., connectance and/or gut content analyses; Briand and Cohen 1987; Spencer and Warren 1996; Townsend et al. 1998; Thompson and Townsend 2005). For instance, biotic indices have been widely used to understand the impacts of human activities on aquatic ecosystems (Resh et al. 1996). However, the method used to generate them is time-consuming (exhaustive identification) and gives little information on ecosystem processes such as energy fluxes and community functioning. Stable nitrogen isotopes can be used as a tool to effectively evaluate food web structure because they take into account complex interactions such as omnivory (Cabana and Rasmussen 1994; Vander Zanden et al. 1997; Post 2002b). Stable nitrogen isotope ratios ($\delta^{15}N$) exhibit a ~3.4‰ enrichment in the heavy isotope (^{15}N) from prey to predator (Minagawa and Wada 1984; Post 2002b). Hence, comparison of the $\delta^{15}N$ value of a consumer relative to the $\delta^{15}N$ value of a baseline organism provides a measure of the number of trophic levels existing between these two organisms (e.g., food chain length). Additionally, examination of the variation in $\delta^{15}N$ with size in the invertebrate community can provide further information on food web structure (Jennings et al. 2002; Maxwell and Jennings 2006). For instance, a community characterized by increasing proportions of predatory invertebrates with body size should exhibit a positive $\delta^{15}N$-size relationship, because predators have a higher trophic level (thus higher $\delta^{15}N$) than primary consumers. Conversely, $\delta^{15}N$ values should remain unchanged with size in a community where predatory invertebrates are scarce. In such a case, invertebrates would be more or less herbivores-omnivores and share similar $\delta^{15}N$ values, irrespective of their size. Additionally, a negative relationship between $\delta^{15}N$ and body size could reflect a community dominated by small predators or parasites (high $\delta^{15}N$ (trophic position)

but smaller size than their prey; Leaper and Huxham 2002) or by large primary consumers with low $\delta^{15}N$ values (Maxwell and Jennings 2006).

Anthropogenic activities should influence $\delta^{15}N$-size relationships by altering community composition. In particular, several large common predatory invertebrates (e.g., Perlidae, Perlodidae (Plecoptera), Corydalidae (Megaloptera)) are sensitive to pollutants and might disappear from impacted sites (Resh et al. 1996; Pelletier and St-Onge 1998; Pelletier 2002), affecting $\delta^{15}N$-size relationships. Thus, their presence might influence $\delta^{15}N$-size relationships and should therefore be considered.

In the present study, we examine whether fish trophic position measured with $\delta^{15}N$ and $\delta^{15}N$-size relationships of the invertebrate community are affected by anthropogenic activities. One particularity of the proposed approach is that the $\delta^{15}N$-size relationships are examined using mean $\delta^{15}N$ values of the total invertebrate biomass of each size class, irrespective of the taxonomic groups of the organisms comprised in it (ataxonomic approach). This approach can be helpful in distinguishing general trophic relationships among size classes of a given community and can reveal relationships that are otherwise obscured by large intra-species variability in $\delta^{15}N$, as found by Jennings et al. (2001). In particular, we examine the effects of chlorophyll *a* (productivity index) and number of industries with pollutant-releasing potential on the watershed (disturbance index) on fish trophic position and slopes of change in $\delta^{15}N$ with size in the invertebrate community. In addition, we examine the effect of predators on trophic position and $\delta^{15}N$-size relationships. More precisely, we examine the effects of 1) increases in overall percent predatory invertebrates in the whole community and 2) increases in the proportions of predatory invertebrates with size (slopes of proportions versus size). We hypothesize that trophic position should either increase or show a hump-back shaped relationship with productivity, and decrease with increasing numbers of industries on the watershed

(Figure 4.1). Furthermore, higher trophic position should be associated with greater increases in the proportions of predatory invertebrates (either in the whole community or in larger size classes (steeper predator-size slopes)). Likewise, $\delta^{15}N$-size slopes should be steeper in more productive systems because of the presence of a greater proportion of predatory invertebrates (e.g., large predatory invertebrates feeding on smaller predators, etc.). Conversely, slopes should be weaker in systems impacted by industrial pollutants, where pollutant-sensitive predators are absent (Figure 4.1).

4.2. Methods

4.2.1. Site selection

Our goal was to select sites showing various levels of system productivity and anthropogenic disturbances. We used chlorophyll *a* concentrations in river water (active chlorophyll *a* in the water column) as a productivity index and number of industries with pollutant-releasing potential on the watershed as a disturbance index. First, chlorophyll *a* is an indicator of algal biomass and reflects the primary productivity of a system. Positive correlations between water column chlorophyll *a* and nutrient concentrations have been well documented in lakes (e.g., Dillon and Rigler 1974; Mazumder and Havens 1998; Brown et al. 2000). Although some studies in rivers and streams have found weaker correlations between nutrients (N and P) and chlorophyll *a* than in lakes, and have attributed them to factors such as shorter water residence time (Soballe and Kimmel 1987; Van Nieuwenhuyse and Jones 1996), several recent studies have found highly significant relationships between sestonic chlorophyll *a* and nutrient concentrations in large rivers (Basu and Pick 1996; Heiskary and Markus 2001; Smith 2003). In particular, Basu and Pick (1996) examined rivers comparable to the ones examined in the current study (similar size and geographic location) and found that 76% of variation in chlorophyll *a* (phytoplankton) was explained by total P. In general, these studies justify the use of

water column chlorophyll *a* as an indicator of primary productivity in large rivers such as those examined in the present study. Second, industries on the watershed can release contaminants in rivers and lakes and a greater number of industries may be associated with greater concentrations of contaminants. In this study, number of industries was used instead of contaminant concentrations in river water because these concentrations were not available (see below).

In order to select our sampling sites, we first compiled data on chlorophyll *a* concentrations and number of industries on the watershed for a total of 76 river sites, from which we subsequently selected a fewer number of sites. Chlorophyll *a* concentrations (mg/m^3) were obtained from long-term water quality monitoring databases of the Ministère de l'Environnement du Québec (2004). We used average chlorophyll *a* concentrations based on a seven-year average (corresponding to available data) from 1996 to 2002.

Recent concentrations of various contaminants in river water could not be obtained. Therefore, we compiled data from previous reports published by the Ministère de l'Environnement du Québec to examine the relationship between concentration of various contaminants in river water and the number of industries on the watershed (Berryman 1996; Berryman and Nadeau 1998; Berryman and Nadeau 1999; Berryman et al. 2002). Using these data, we established a correlation between the concentration of several contaminants in river water and the number of industries on the watershed (industries qualified having a "potential to pollute aquatic systems due to the quality and quantity of their discharges" (Dartois and Daboval 2003), which include wood and pulp industry, chemistry, metallurgy, textiles, food industry, and oil refineries). More exactly, we performed a principal components analysis on the water chemistry data shown in these reports and obtained a first axis (PC1) characterized by industrial pollutants such as copper, nickel and lead (Table 4.1). We then plotted the factor scores of this axis against the total number of industries on the

watershed shown in these reports. The relationship between the number of industries (log-transformed) and PC1 was modest, but significant ($n = 19$, $r^2 = 0.31$, $p < 0.05$; higher concentrations found in more industrial watersheds). This supported our decision to use the total number of industries on the watershed as an indicator of industrial contaminants in water (e.g., disturbance). Finally, the number of industries (types cited above) on watersheds upstream of each potential study site (76 sites) was estimated using databases from the Centre de Recherche Industrielle du Québec (2003) for the year 2003 (spring).

After computing total number of industries and chlorophyll *a* concentrations for the 76 river sites for which all data were available, we selected a fewer number of sites that showed a wide range of chlorophyll *a* concentrations and numbers of industries. Overall, 23 sites were selected. These sites were located within 11 subwatersheds of the Saint-Lawrence River watershed (Québec, Canada; Figure 4.3), and catchments ranged from 175 to 42 820 km².

4.2.2. Land use and water quality data

Delineation of the 23 selected watersheds and land use characterization are detailed in Anderson and Cabana (2005, 2006). Number of industries on watersheds was estimated as shown above and ranged from 0 to 432 (mean = 84, s.d. = 120). Total number of industries was also divided by water discharge to yield an industrial gradient corrected by river discharge. Water discharge was estimated for each study site using a regression equation between watershed area and water discharge ($r^2 = 0.95$, $p < 0.0001$) previously obtained for 24 sites located on the same rivers examined in the present study (C. Anderson, Unpublished). Discharge ranged from 4.5 to 641 $m^3 s^{-1}$ (mean = 88.4, s.d. = 158.7). Chlorophyll *a* concentrations (water column; mg/m^3) were averaged by study sites using data from august 1998 to august 2003 (average of the five years preceding the sampling month) provided by the Ministère de l'Environnement du Québec (2004). Measurements were taken, on

average, once or twice per month for each study site during the summer period (May to October). The total number of chlorophyll *a* samples by site ranged from 15 to 38. Chlorophyll *a* concentrations ranged from 0.66 to 16.92 mg/m^3 (mean = 4.96, s.d. = 4.00).

4.2.3. Sampling and identification

Invertebrates and fish were collected in August 2003. Invertebrates were collected with a Surber net (0.1 m^2; 0.6 mm mesh size; four replicates taken at each site) and a D-frame aquatic net (1 mm mesh size). Fish were captured by electro fishing. Samples were kept in coolers and frozen within eight hours and then thawed for sorting and identification. Invertebrates caught with the D-frame net were sorted and identified to family or genus. Invertebrates caught with the Surber net were sorted by size class by washing organisms through a series of 10 brass-frame laboratory sieves (mesh sizes: 0.5, 0.71, 0.85, 1, 1.41, 2, 2.83, 3.36, 4, and 8 mm), and identified to family. Invertebrates that fell through the 0.71 mm mesh size sieve but which were retained by the 0.5 mm mesh size sieve were kept in all analyses, despite the fact that the Surber net had a mesh size of 0.6 mm. This could have induced certain variability in the 0.5 mm size class results. However, a laboratory test using a smaller sieve (0.25 mm mesh size) showed that a large proportion of smaller sized invertebrates – which also fell through the 0.5 mm mesh size sieve – were caught by the 0.6 mm-mesh Surber (personnal observations), suggesting that the invertebrate density of the 0.5 mesh-size sieve might not be as largely underestimated as initially expected.

Invertebrates were also classified into seven groups (primary consumer, predator, omnivore, parasite, chironomid (identified to the family), nematoda (identified to the family), and zooplankton) according to Merritt and Cummins' (1996) and Thorp and Covich's (1991) classifications. Over 24 300 organisms were identified. Predators, which made up 2.4% of all organisms captured, were principally

composed of Plecoptera (32%; almost exclusively Perlidae) and Diptera (27%; mostly Empididae and Athericidae). Odonata and water mites (Hydrachnidia) also composed a large part of this group (14% and 10% respectively). Fish were identified to species (Scott and Crossman 1974). Captured fish were small specimens of four non-piscivorous species (Longnose dace (*Rhinichthys cataractae*), blacknose dace (*Rhinichthys atratulus*), Johnny darter (*Etheostoma nigrum*) and logperch (*Percina caprodes*)) and juvenile smallmouth bass (*Micropterus dolomieui*; ≤ 103 mm). These species were selected because they were well distributed throughout study sites. A total of 121 individual fish were captured and used for isotopic analyses (2-11 individuals per site; 1-4 species per site). Their overall size (total length; measured after freezing) ranged from 37 to 117 mm (mean = 68 mm, s.d. = 19 mm).

Once identified, all samples were dried at 60 °C for at least 48 hours and ground into a homogenous powder. Non-animal materials were removed from the samples prior to the analyses. Invertebrates collected with the Surber net were pooled by size class for isotopic analyses. Two samples randomly drawn from the four Surber samples collected on the field were analysed for each study site. Surber replicates showing too small amounts of material for isotopic analyses were pooled for some sites (replicates of the 0.5, 0.71 and 0.85 mm classes were combined for 15, 12, and 8 sites, respectively). Other invertebrates (D-frame net), which were used in the trophic position estimates, were pooled and analysed by genus or family. Invertebrates were used whole, except molluscs which were removed from their shells. In the case of fish, small sections of muscle tissue were taken from individual fish and sent for isotopic analysis. Invertebrates caught with Surber nets were used to derive δ^{15}N-size slopes of the communities examined, whereas invertebrates (primary consumers) collected using the D-frame nets and fish were used to estimate fish trophic position.

Isotopic analyses were performed at the University of New Brunswick with a Finnigan-Mat Delta Plus mass spectrometer. Isotopic ratios were expressed following the standard equation:

$$\delta^{15}N = [(^{15}N/^{14}N_{sample}/^{15}N/^{14}N_{standard}) - 1] * 1000 \quad (1)$$

where isotopic ratios are expressed as the relative parts per thousand (‰) ratio between a sample and a known reference material, which, by convention, is atmospheric nitrogen (N_2). A total of 610 samples were analysed and used in the present study. 54 samples were analysed in duplicate and showed a mean standard deviation of 0.21‰.

4.2.4. Trophic position estimates

In a previous study, we showed that the use of baseline organisms belonging to various functional feeding and taxonomic groups could lead to biases in trophic position estimates (Anderson and Cabana 2007). In the present study, we used the procedure detailed in Anderson and Cabana (2007) to estimate fish trophic position. Briefly, ubiquitous primary consumers (three scraper families) with low $\delta^{15}N$ values were used as baseline indicators. In addition we also included $\delta^{15}N$ values of hydropsychids (Trichoptera: Hydropsychidae) in the baseline $\delta^{15}N$ estimates because they were dominant in numerous sites and their exclusion would have lead to a smaller number of sites for which trophic position could have been estimated. Before computing baseline $\delta^{15}N$, we corrected Hydropsychidae $\delta^{15}N$ values toward Psephenidae (Coleoptera) $\delta^{15}N$ as was done in Anderson and Cabana (2007) for two of the scraper families used. The mean difference between hydropsychids and psephenids calculated using the dataset of Anderson and Cabana (2007), was of 1.42 ‰ (paired t-test, Bonferroni corrected; $p < 0.0001$). We thus used this value to correct Hydropsychidae $\delta^{15}N$ downwards toward Psephenidae $\delta^{15}N$. Last, $\delta^{15}N$ values

of Ephemerellidae (*Drunella*), Heptageniidae (*Heptagenia* and *Stenonema*), and Hydropsychidae were all corrected towards Psephenidae $\delta^{15}N$, as shown in Anderson and Cabana (2007), and $\delta^{15}N$ values of these four families were averaged by site to yield baseline $\delta^{15}N$.

Using this baseline $\delta^{15}N$ value, we estimated trophic position following the equation:

$$\text{Trophic Position}_{\text{consumer}} = ((\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})/ 3.4) + 2 \qquad (2)$$

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value of the consumer for which the trophic position is estimated, $\delta^{15}N_{\text{baseline}}$ is the $\delta^{15}N$ value of the baseline organism, and 2 is the expected trophic position of the organism used to estimate baseline $\delta^{15}N$ (e.g., an herbivore).

4.2.5. Statistical analyses

Effects of fish species and fish size on trophic position were examined using a one-way analysis of variance and a linear regression, respectively. Spatial variation in trophic position was also examined with a one-way Anova using site as a factor. Percent predatory invertebrates was calculated on the total number of organisms collected by size class and for the entire invertebrate community. Slopes of the relationship between $\delta^{15}N$ and size (log-transformed), and slopes of change in percent predators with size were computed using linear regressions. $\delta^{15}N$ values and percent predatory invertebrates were averaged by size class for each site (two replicates averaged). Changes in $\delta^{15}N$ and percent predators with size among sites were examined using covariance analyses with log size and study sites as factors.

Relationships between trophic position and δ^{15}N-size slopes, and relationships between these two dependent variables and the independent variables (chlorophyll *a*, number of industries, percentage of predators, and predator-size slopes) were examined using simple linear regressions. Multiple linear regressions were used to evaluate the combined effect of 1) chlorophyll *a* and number of industries and 2) predatory invertebrates on trophic position and δ^{15}N-size slopes, respectively.

Statistical analyses were performed using SYSTAT (Version 8.00, SPSS Inc. 1998) and SAS (Version 8.0, SAS Institute Inc. 1999). In order to meet regression analysis assumptions (Zar 1999; Tabachnick and Fidell 2001), size and number of industries (and number of industries/discharge) were log-transformed. Chlorophyll *a* concentrations were square-root transformed and all percentages (predators) were arcsin transformed.

4.3. Results

4.3.1. Trophic position and δ^{15}N-size relationships

Fish trophic position varied greatly across sampling sites, ranging from 2.39 to 3.89 trophic levels. No significant effects of fish species (One-way Anova, $p > 0.05$) and size (linear regression, $p > 0.05$) were found on trophic position, enabling the use of fish trophic position without correcting for size or species effect. An analysis of variance showed that 71% ($F = 10.847$, $df = 22,99$, $p < 0.0001$) of the variation in fish trophic position was attributable to site effects, suggesting heterogeneity in food web structure among our study sites.

δ^{15}N values of invertebrates increased significantly with size in 14 of the 23 study sites ($p > 0.05$ Table 4.2; Figure 4.4). Slopes of these 14 relationships spanned from 0.54 to 6.78. Of the remaining 9 sites (Slopes from -0.99 to 1.1), 8 showed no

significant trend ($p > 0.05$), whereas one site showed a trend towards a decrease in $\delta^{15}N$ with size ($r^2 = 0.35$, $p = 0.07$; Site C8 in table 4.2). A covariance analysis using log size and study sites as factors confirmed that change in $\delta^{15}N$ with size was significantly different among the 23 study sites (interaction of site and log size on $\delta^{15}N$: $F = 3.57$, $df = 22,198$, $p < 0.0001$). The highest slope (6.78) measured in one site was clearly an outlier. This high slope was potentially caused by the presence of small zooplankton (personal observation) with low $\delta^{15}N$ values in the food web likely originating from a reservoir (dam) located upstream of the sampling site (~500 m). This site was removed from subsequent analyses.

Trophic positions of fish and slopes of $\delta^{15}N$-size relationships of the invertebrate community were not significantly correlated ($p > 0.05$).

4.3.2. Productivity and disturbance

Trophic position of fish was not significantly correlated with chlorophyll *a* concentrations measured in water ($p > 0.05$, Figure 4.5a). However, slopes of $\delta^{15}N$-size were modestly, but significantly correlated with chlorophyll *a* concentrations ($r^2 = 0.22$, $p < 0.05$), $\delta^{15}N$ values showing greater increases with size in more productive systems (Figure 4.5b). Industrial activities did not significantly affect trophic position or $\delta^{15}N$-size relationships (log industries (Figure 4.6) or log industries/watershed area (not shown): $p > 0.05$).

However, combining total number of industries on the watershed to chlorophyll *a* concentrations (multiple regression) helped explain a larger proportion of the variation in $\delta^{15}N$ with size. In particular, slopes of $\delta^{15}N$-size increased with productivity and decreased as number of industries increased. The multiple regression obtained ($r^2 = 0.43$; $p < 0.01$) is:

$$\text{Slope } \delta^{15}\text{N-size} = -0.08 + 0.86\ (\text{chlorophyll } a^{0.5}) - 0.67\ (\log_{10} \text{number of industries}) \quad (3)$$

Both variables contributed significantly to the multiple regression equation ($p < 0.05$; s.e. chlorophyll $a = 0.23$; s.e. industries = 0.25).

4.3.3. Functional diversity

Percent predatory invertebrates found in the invertebrate community varied from 0.1 to 14.7% across sites and slopes of change in percent (arcsin transformed) predatory invertebrates with size ranged from -14.1 to 46.0. These slopes varied significantly among sites (Analysis of covariance, interaction of site and log size: $p < 0.0001$; $r^2 = 0.47$, $F = 4.95$, $df = 22,206$).

No significant relationship was found between trophic position and percent predatory invertebrates across sites ($p > 0.05$). δ^{15}N-size slopes, however, became slightly steeper ($r^2 = 0.18$, p being borderline at 0.053) as the proportion of percent predatory invertebrates increased with size (e.g., steeper slopes of percent predatory invertebrates-size; Figure 4.7b). Since we hypothesized that δ^{15}N-size slopes would decrease in disturbed sites but increase with greater proportions of predators, we also examined the above relationship with leeches (Annelida: Hirudinea) removed from the predatory invertebrate group. Indeed, leeches are large predatory invertebrates which potentially show high δ^{15}N values, but which are known to be pollution-tolerant (Resh et al. 1996). Hence, they could both be associated with higher slopes (more predators) and weaker slopes (disturbed sites) at the same time, and might induce noise in the relationship between predator-size slopes and δ^{15}N-size slopes. The relationship between percent predatory invertebrate-size slopes and δ^{15}N-size slopes was improved when leeches were removed ($r^2 = 0.27$, $p = 0.014$), supporting our hypothesis.

4.4. Discussion

4.4.1. Trophic position and δ^{15}N-size relationships

Trophic position estimates of small fish were highly and significantly variable among sites, suggesting spatial heterogeneity in food web structure and/or in fish feeding behaviour. In particular, fish trophic position ranged from 2.39 (mostly feeding on primary producers) to 3.89 trophic levels (mostly feeding on secondary consumers). Large variability in trophic position estimates of both forage and piscivorous fish has been reported in previous studies (Vander Zanden and Rasmussen 1996; Fry et al. 1999; Vander Zanden et al. 2000). In particular, Vander Zanden et al. (2000) found variation in trophic position of invertebrate-feeding fish (including ciscos, littoral prey fish, and sculpins) of 2 trophic levels (~2.7–4.6) across 13 Canadian lakes. In addition, in a previous study conducted on the same watersheds examined in the present study, but using a greater number of sites (87 river sites; Anderson and Cabana 2007), we obtained a similar range in trophic position (2.56 to 4.54). These variations were similar to the range observed in the present study. In general, the variation obtained in our 23 study sites seems representative of the variation in lake and river forage fish trophic position in eastern Canada.

Variability in fish trophic position can be attributed to omnivory. The ability of fish to feed upon different trophic levels can generate variability in trophic position. For instance, Cabana and Rasmussen (1994) have found shifts of up to 1 trophic level in lake trout (*Salvelinus namaycush*) trophic position measured using δ^{15}N when they fed on herbivorous zooplankton, mysids, or forage fish. Thus, the ability to feed on primary producers, primary consumers, or secondary consumers (within or across sites) could explain the variability observed in the trophic position estimates of the fish species used in the current study. Also, it is important to bear in mind that part of the observed variability in δ^{15}N (both in the trophic position and δ^{15}N-size slope estimates) could be caused by differential fractionation of ^{15}N among

sites and species (see discussion in Anderson and Cabana 2007). However, as observed in Anderson and Cabana (2007), the use of a single fractionation value throughout the food web (e.g. 3.4‰) can still provide a good general picture of trophic interactions in a community.

δ^{15}N-size slopes were highly variable across sites and also suggest heterogeneity in food web structure. Indeed, positive slopes suggest increasing proportions of predatory or omnivorous organisms in the community as size increases. Conversely, the absence of change in δ^{15}N with size reflects a community dominated by organisms feeding on the same resources, irrespective of their size (e.g., larger organisms do not have a higher trophic position than smaller ones and thus potentially feed on similar resources).

Several studies have found increases in δ^{15}N or trophic position with size in benthic (France et al. 1998; Jennings et al. 2002) and zooplanktonic communities (Fry and Quinones 1994; Montoya et al. 2002). In particular, using an ataxonomic approach involving pooling all individuals by size, as in the present study, Jennings et al. (2002) found increases in δ^{15}N values with size in aquatic invertebrates collected in the North Sea. Increases in δ^{15}N with size in aquatic communities are expected following studies such as Wilson (1975) and Cohen et al. (1993), who proposed that, as size of organisms increase, so does their potential to feed on other animals. Hence, the size of animals has often been used as an indicator of their potential trophic position. However, the absence of relationship between δ^{15}N and size or the presence of a negative relationship suggests that trophic position does not always systematically increase with size in a community. Such absence of relationship between δ^{15}N and size or decreases in δ^{15}N values with size have been observed by Maxwell and Jennings (2006) for benthic fauna collected in the North Sea (all fauna combined). The presence of small polychaetes with high δ^{15}N values and large

bivalves with low $\delta^{15}N$ values explained these negative slopes. In such a case, smaller organisms were more predatory than larger ones, which yielded negative slopes. Similarly, Leaper and Huxham (2002) showed that the presence of parasites (predators that are smaller than their prey) in a given system could induce decreases in trophic position with size. Overall, these studies show that trophic position does not necessarily increase with size, depending on the structure of the food web (e.g., presence of small predators or parasites versus large predators). Our results support this finding by showing that $\delta^{15}N$ does not always increase with size in lotic communities. In particular, they show that variation in trophic position ($\delta^{15}N$) with size in a community can be different from one site to another (spatial variation). We found that this variability depends, in part, on the presence of large predatory invertebrates (which may themselves be influenced by anthropogenic activities).

Fish trophic positions and slopes of $\delta^{15}N$-size relationships of the invertebrate community were not significantly correlated. This finding is not concordant with our initial predictions. We predicted that steeper slopes of $\delta^{15}N$-size in the invertebrate community would be associated with higher trophic position of fish. Indeed, if invertebrates tend to show greater trophic position with size, fish, which feed on these invertebrates, should also exhibit a greater trophic position. The absence of a correlation between trophic position and $\delta^{15}N$-size slopes can be explained by fish feeding behaviour. First, even though invertebrates exhibit higher trophic position at a given size class in some sites, fish might not feed on these large invertebrates because of feeding preferences. Several studies have examined fish feeding preferences, with a particular interest in the size of preferred prey. Although many studies found that invertebrate-feeding fish preferentially ate large prey (Brooks 1968; Werner and Hall 1974; Bartell 1982), several researchers observed humped size preference (preference for intermediate-sized prey) or preference for smaller prey (Hansen and Wahl 1981; Teska and Behmer 1981; Bence and Murdoch 1986). In

particular, these latter studies examined relationships between prey and predators relatively close in size, and are potentially more comparable to the organisms examined in the present study. Perhaps the relatively small size of fish (mean size of 68 mm) compared to large invertebrates (up to 8 mm sieve size: equivalent to ~21.5 mm mean body length) could explain the lack of relationship between $\delta^{15}N$-size relationships in the invertebrate community and fish trophic position. Unger and Lewis (1983) have examined the relationship between fish length and gape size of a small (16-84 mm body length) planktivorous fish. They found a gape size of ~4 mm for fish of ~68 mm. This finding supports our contention that gape size of the invertebrate-feeding fish we selected might preclude them from eating large invertebrates (≥4 mm sieve size) with higher trophic positions. In a parallel study (Anderson and Cabana, Unpublished), we found that the average size of invertebrates found in the guts of the five fish species selected in the current study (stomach contents of 99 fish collected in 6 of the present study's sites: sites with low, medium and high trophic positions, respectively) was only of 0.62 mm (sieve size). Moreover, the largest invertebrate size class found in the fish stomachs was 3.36 mm (sieve size; in 3 out of 99 fish). Although these observations consist of a snapshot of fish gut content, they support the contention that the fish used in the current study seldom feed on very large invertebrates (with potentially high trophic position).

Lastly, the lack of relationship between trophic position and $\delta^{15}N$-size slopes could be attributable in part to the fact that both variables were measured only once during the year (August). Small-bodied organisms might show more variation in their $\delta^{15}N$ values than larger ones throughout the year, affecting significantly $\delta^{15}N$-size relationships. Furthermore, emergence of insects might generate changes in the trophic structure of the community, altering again $\delta^{15}N$-size slopes. The use of annual mean $\delta^{15}N$-size slopes and trophic positions (several sampling dates throughout the

year) in future studies could yield further insights on how year-round trophic position and $\delta^{15}N$-size slopes are correlated with one another.

Overall, fish trophic position and $\delta^{15}N$-size slopes of the invertebrate community seem to represent two different measurements of food web structure. $\delta^{15}N$-size relationships reflect changes in the trophic structure of the entire invertebrate community, whereas fish trophic position does not necessarily integrate changes in the trophic structure of the invertebrate community (unlike what we initially expected). Hence, $\delta^{15}N$-size relationships are potentially better tools to measure the effect of various environmental factors on food web structure than fish trophic position, which is too influenced by fish feeding preferences to be a true and sole indicator of impacts of external stressors on the food web.

4.4.2. Determinants of food chain length

Although sites examined in the present study ranged from oligotrophic to eutrophic, we did not find any relationship between fish trophic position and productivity. However, $\delta^{15}N$-size slopes became steeper in more productive systems (higher chlorophyll *a* concentrations), supporting the hypothesis that richer systems can support longer food chains. Indeed, faster increases in $\delta^{15}N$ with size suggest that organisms of a given size exhibit a higher trophic position than those found in sites where $\delta^{15}N$ does not increase quickly with size. The fact that $\delta^{15}N$-size slopes were also slightly steeper when the proportion of predators increased in larger size classes supports this interpretation. In such cases, there is an increased possibility for large predators to feed on medium-sized predators which feed themselves on small-sized predators (thus lengthening the food chain). In general, increased productivity potentially supports greater proportions of predators of various size classes, which yield greater $\delta^{15}N$ values in large size classes where these predators are present.

Previous laboratory and field studies examining the effect of productivity on food chain length have found contrasting results. Several traditional studies (not using stable nitrogen isotopes to measure trophic position) found significant effects of productivity on the lengthening of aquatic food chains (Jenkins et al. 1992; Townsend et al. 1998; Thompson and Townsend 2005). Others found non significant trends towards longer chains in more productive systems (Pimm and Kitching 1987; Spencer and Warren 1996). Additionally, Persson et al. (1992) found a hump-back relationship between food chain length and productivity. They found that food chain length first increased with productivity (chlorophyll *a*) in lakes, but than started to decrease in the most productive lakes. This hump-back relationship could be explained by the fact that increased productivity generates greater potential food chains (more energy), but at the same time, this potential can reduce the dynamic stability of the food web and thus shorten food chains (Morin and Lawler 1995). It thus supports the intermediate disturbance hypothesis, where unproductive systems do not have enough energy to support long food chains, but where highly productive systems are unstable and vulnerable to disturbances (Jenkins et al. 1992, for example). We did not find any evidence for a humped relationship between trophic position or slopes of δ^{15}N-size and chlorophyll *a*. However, Persson et al. (1992) measured food chain length up to piscivorous fish, whereas we only measured trophic position of insectivorous fish.

In other studies using stable nitrogen isotopes, productivity generally revealed to be a poor predictor of fish trophic position. For instance, Post (2000) did not find any relationship between productivity and trophic position, whereas Jepsen and Winemiller (2002) found higher fish trophic position in poorer systems. However, this latter study only examined 4 sites. Finally, Vander Zanden et al. (1999) found a significant, but relatively small effect of productivity (measured as Secchi depth) on

lake trout trophic position. Lake trout had higher trophic position in more productive systems.

Overall, we found a significant relationship between δ^{15}N-size slopes and productivity. However, this relationship was modest. Other factors such as disturbance (e.g., pollution originating from industrial activities) may have dampened the effect of productivity. Indeed, adding industrial activities to chlorophyll *a* in a multiple regression helped explain a greater proportion of the variability in changes of δ^{15}N with size. Similarly, productivity may have obscured the effects of disturbance, because industries alone did not have a significant effect on δ^{15}N-size relationships, but became significant when chlorophyll *a* was considered. This suggests that these two variables are entangled among our study sites and tend to hamper the effect of one another. Overall, using a multiple regression, we found that steeper δ^{15}N-size slopes were associated with higher chlorophyll *a* concentrations, but weaker slopes were associated with a greater number of industries (with pollutant-releasing potential) on the watershed.

The lower slopes of δ^{15}N with size in more industrial watersheds suggest shorter food chains. In these sites, larger organisms do not show much higher trophic positions than smaller ones. This could be due to the lack of large predatory invertebrates. First, several large predatory invertebrate species (e.g., Perlidae and Perlodidae (Plecoptera), Corydalidae (Megaloptera)) tend to be more sensitive to pollutants than smaller, more tolerant species such as chironomids or oligochaetes (Resh et al. 1996; Pelletier and St-Onge 1998; Pelletier 2002; Voshell 2002). Additionally, as suggested by Menge and Sutherland (1987) large organisms are potentially more mobile than smaller ones and might leave polluted (stressed) systems. Hence, loss of large predatory invertebrates (within our size spectrum) in polluted systems through death or migration may explain the weaker slopes observed.

A few experimental studies have observed shorter and simplified food chains in disturbed ecosystems (Jenkins et al. 1992; Sherwood et al. 2002). In particular, Sherwood et al. (2002) examined the impact of industrial contaminants on food web structure. They found that food web leading to yellow perch in metal-polluted lakes was extremely simplified compared with reference lakes. This simplification was due to the disappearance of benthic invertebrates (successively larger prey types not available for perch in polluted lakes). Other studies have also found significant effects of industrial activities and contaminants on the loss of aquatic invertebrate species (Garie and McIntosh 1986; Ford 1989 and references therein; Pelletier 2002), and support our hypothesis of food chain length reduction with increasing industrial pollution.

Finally, impairment of predation by fish has been documented in contaminant-polluted systems (Atchison et al. 1987; Brown et al. 1987; Weis et al. 2000). Fish in such systems fed lower in the food web than in reference sites, thus shortening food chain length. The lack of relationship between fish trophic position and industrial activities in our study (either simple or multiple regressions) does not support the theory that fish feeding behaviour is impaired in polluted systems (lower trophic position).

4.5. Conclusion

Overall, $\delta^{15}N$-size slopes of the invertebrate community were significantly altered by human activities. In particular, $\delta^{15}N$ values showed greater increases with size in productive systems than in disturbed systems. Slopes of change in $\delta^{15}N$ with size were also greater when the proportion of predators increased in larger size classes. These results suggest that when productivity is high and disturbance is low, food chains tend to be longer (e.g., higher $\delta^{15}N$ value –trophic position– for a given

size class). They also suggest that $\delta^{15}N$-size relationships of invertebrate communities may be used as indicators of food web structure alteration by human activities. Conversely, fish trophic position seemed to be too influenced by fish feeding behaviour to provide a good indicator of food web structure.

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Table 4.1. PC1 scores for contaminants related to industrial activities found in river water (n = 19). Type of transformations on variables prior to statistical testing are shown (transformations based on Tabachnick and Fidell 2001). Signs of factor scores of elements that were transformed using 'reflect' or 'inverse' should be reversed (e.g., copper is positive on PC1 because its inverse is negative).

Contaminant	Transformation	PC1 score
PCB	Inverse	0.143
Aluminium	Square root	0.828
Chromium	Log	0.892
Copper	Inverse	-0.641
Iron	None	0.029
Magnesium	None	0.474
Manganese	Square root	-0.299
Mercury	Square root	0.289
Nickel	Log	0.906
Lead	Log	0.904
Vanadium	Reflect; Square root	-0.418
Zinc	Log	0.180
Fatty and resinic acids	Log	-0.295

Table 4.2. Statistics for the $\delta^{15}N$-size relationships of the 23 study sites.

Study site	$\delta^{15}N$-size slope	r^2
A3	-0.37	0.05
As1	0.89	0.56**
As2	0.09	0.00
As5	-0.99	0.18
As7	2.23	0.57**
B2	1.53	0.68***
Bc1	1.77	0.65**
C5	0.96	0.51*
C6	0.54	0.52*
C8	-0.97	0.35
E1	0.88	0.17
F10	6.78	0.89***
F14	1.44	0.65**
F4	1.09	0.29
L1	1.04	0.47*
M1	-0.16	0.02
M3	1.02	0.80**
M5	-0.33	0.02
N2	0.89	0.70**
N5	2.76	0.82***
Y4	0.20	0.03
Y5	1.29	0.89***
Y8	1.67	0.62**

* = $p < 0.05$; ** = $p < 0.01$, *** = $p < 0.001$

4.8. Figure captions

Figure 4.1. Expected relationships between two food chain length indices (trophic position and slopes of δ^{15}N-size) and a) productivity and b) disturbances related to industrial activities.

Figure 4.2. Chlorophyll *a* concentrations and number of industries with pollutant-releasing potential for the 76 potential study sites. The 23 selected sites are represented by closed circles.

Figure 4.3. Study sites sampled in summer 2003.

Figure 4.4. Relationships between δ^{15}N and size class for sites where relationships were significant ($p < 0.05$). Note that one site considered as an outlier was removed from the figure (slope = 6.8; see text). Relationships were scaled to a common intercept by subtracting the δ^{15}N value of the smallest size class from all δ^{15}N values (difference in δ^{15}N) for each study site. Regression lines are represented by solid lines.

Figure 4.5. Relationship between a) trophic position and b) slopes of δ^{15}N-size and chlorophyll *a* concentrations. The linear regression equation between δ^{15}N-size and chlorophyll *a* concentrations is: Slope δ^{15}N-size = -0.28 + 0.52 chlorophyll $a^{0.5}$. Regression lines are represented by solid lines.

Figure 4.6. Relationship between a) trophic position and b) slopes of δ^{15}N-size and number of industries on the watershed. Regression lines are represented by solid lines.

Figure 4.7. Relationships between slope of $\delta^{15}N$-size and a) arcsin transformed percent predatory invertebrates with size, and b) arcsin transformed percent predatory invertebrates excluding leeches with size. Regression lines are represented by solid lines.

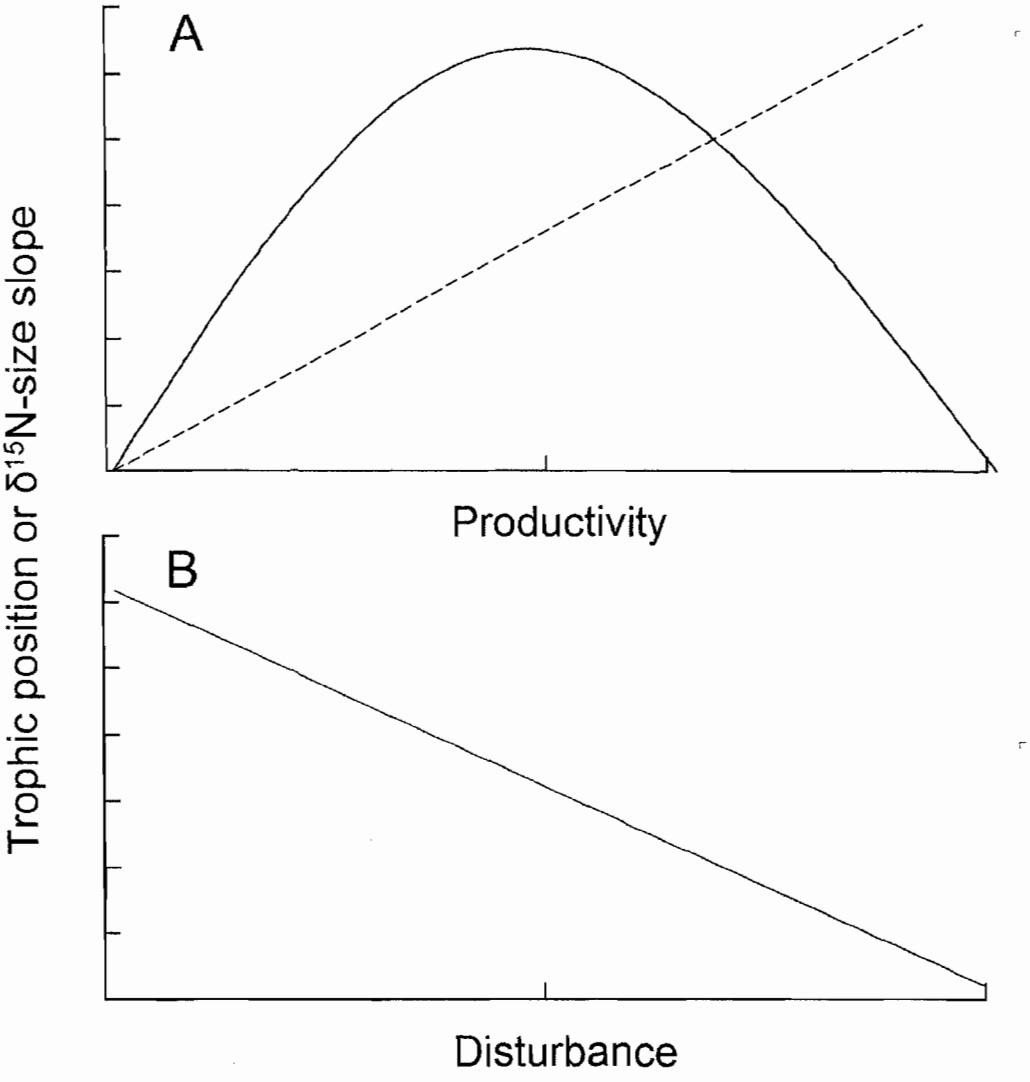
A
Trophic position or δ15N-size slope
Productivity
B
Disturbance

Figure 4.1.

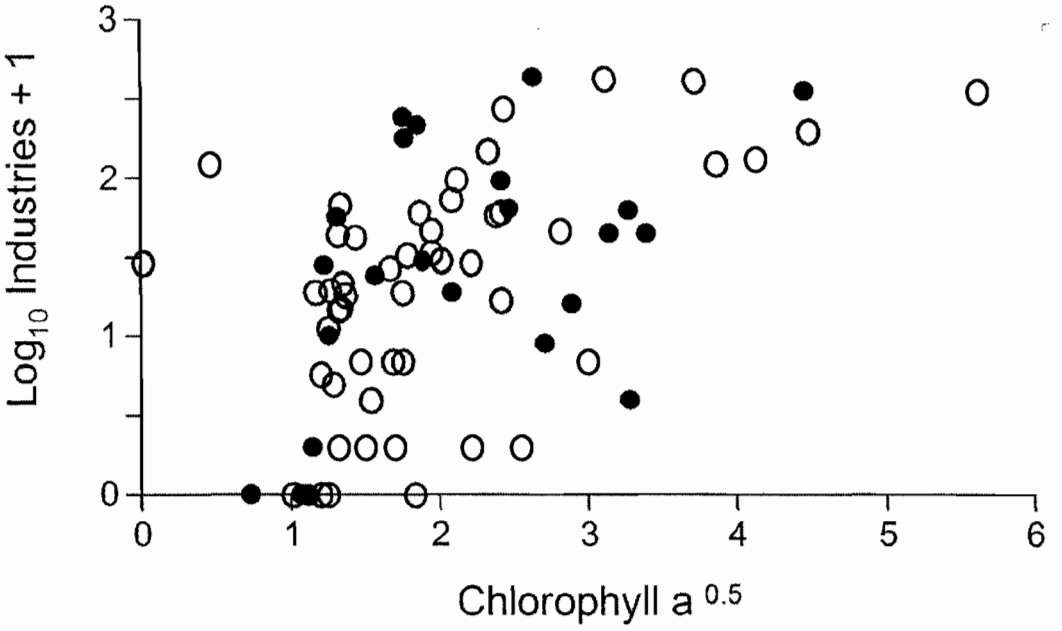

Figure 4.2.

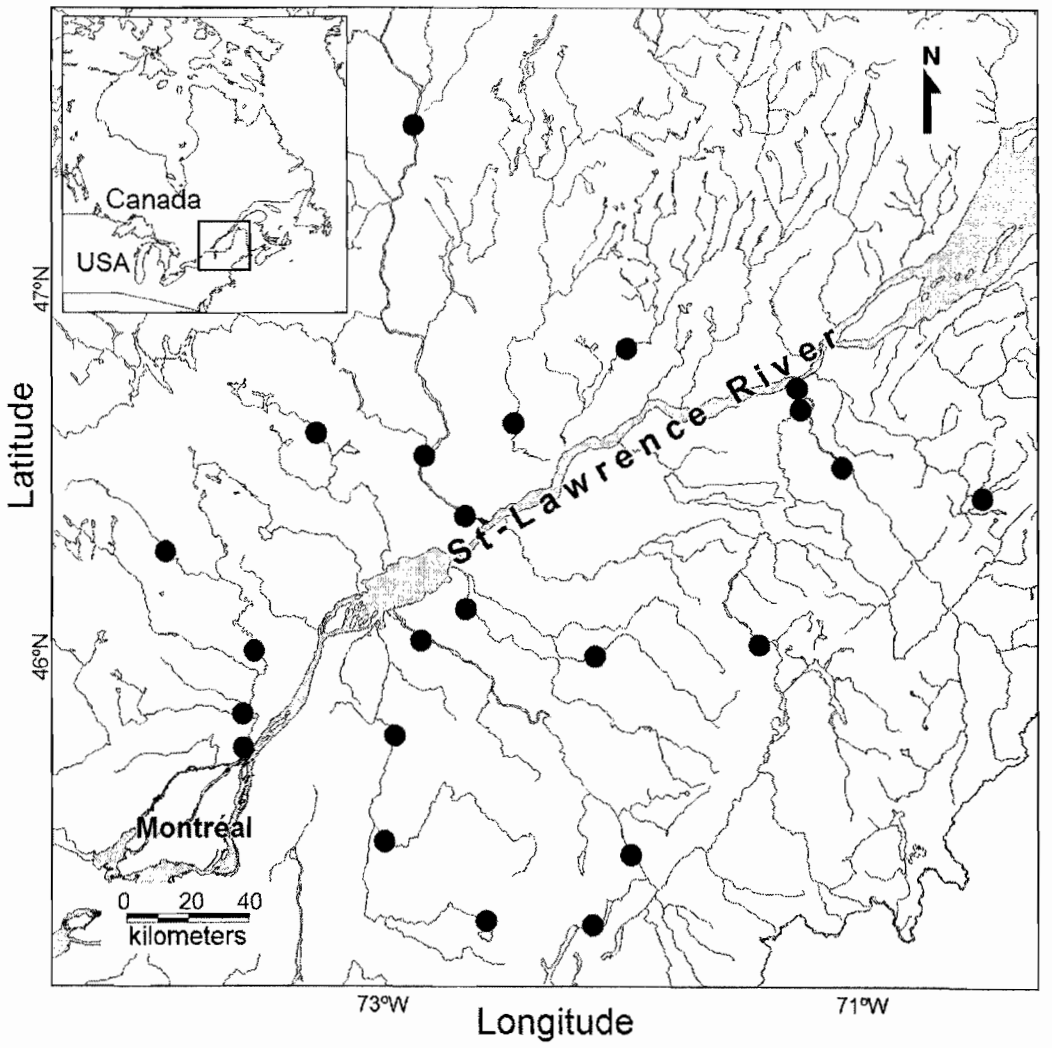
Canada
USA
N
St-Lawrence River
Montréal
0 20 40
kilometers
47°N
46°N
73°W
71°W
Latitude
Longitude

Figure 4.3.

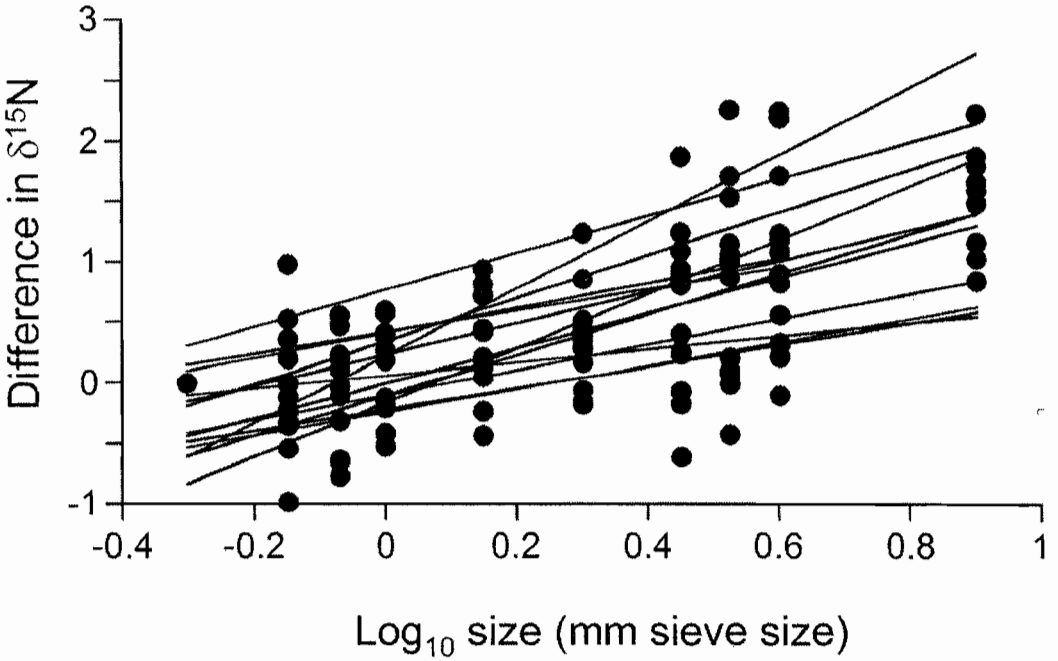
Difference in δ15N
3
2
1
0
-1
-0.4
-0.2
0
0.2
0.4
0.6
0.8
1
Log10 size (mm sieve size)

Figure 4.4.

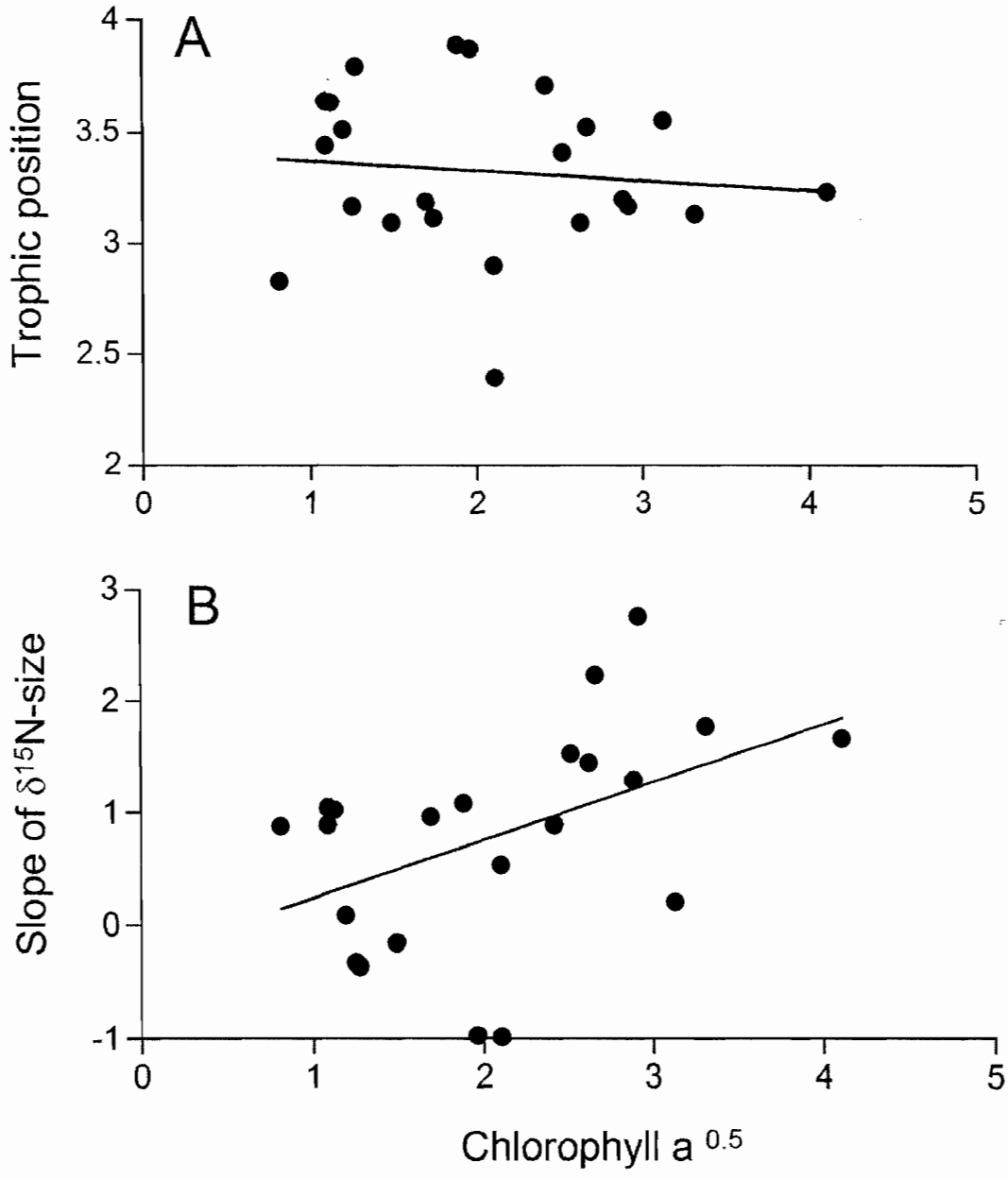
A
Trophic position
4
3.5
3
2.5
2
0
1
2
3
4
5
B
Slope of δ15N-size
3
2
1
0
-1
0
1
2
3
4
5
Chlorophyll a 0.5

Figure 4.5.

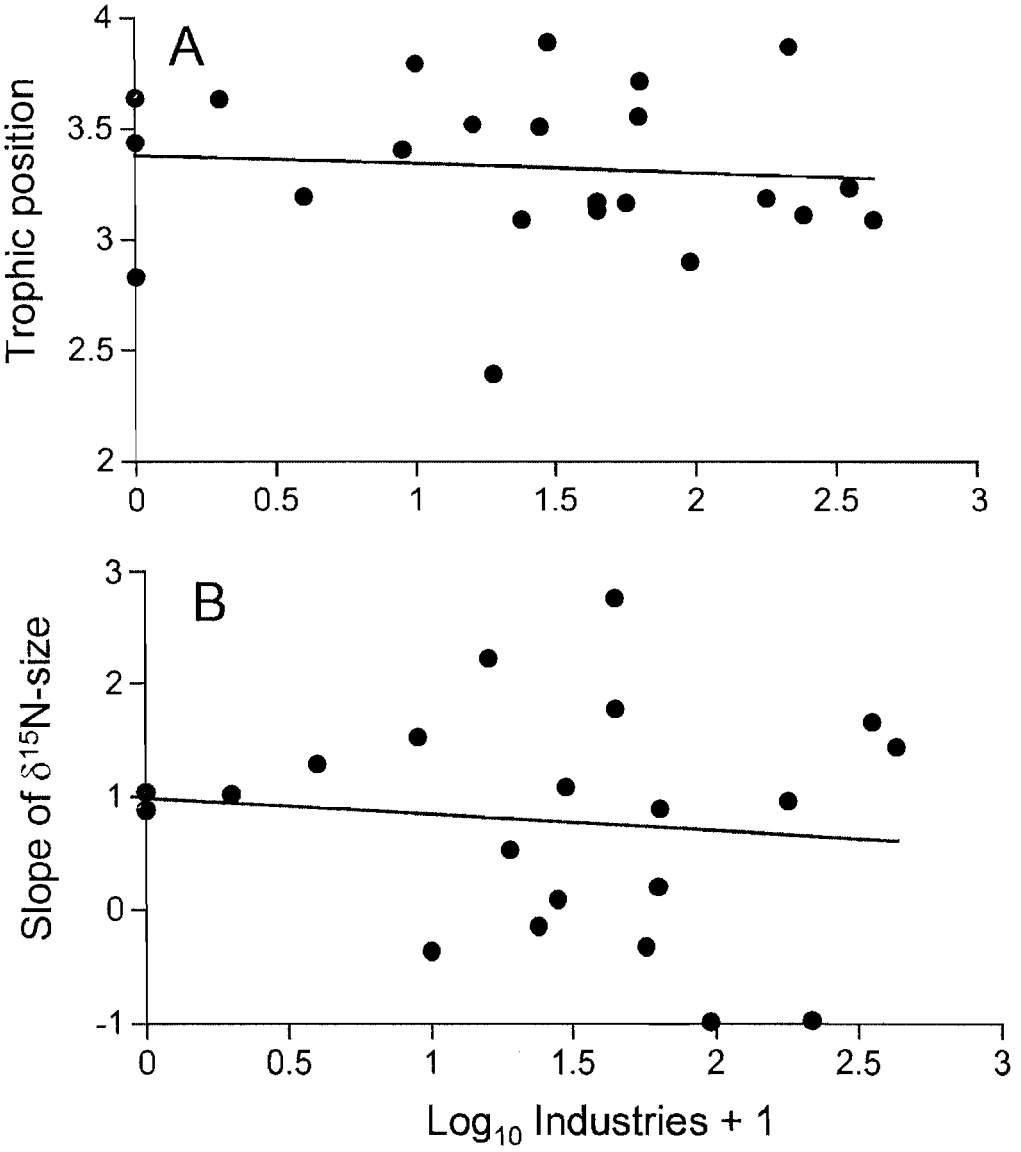
A
Trophic position
4
3.5
3
2.5
2
0
0.5
1
1.5
2
2.5
3
B
Slope of δ15N-size
3
2
1
0
-1
0
0.5
1
1.5
2
2.5
3
Log10 Industries + 1

Figure 4.6.

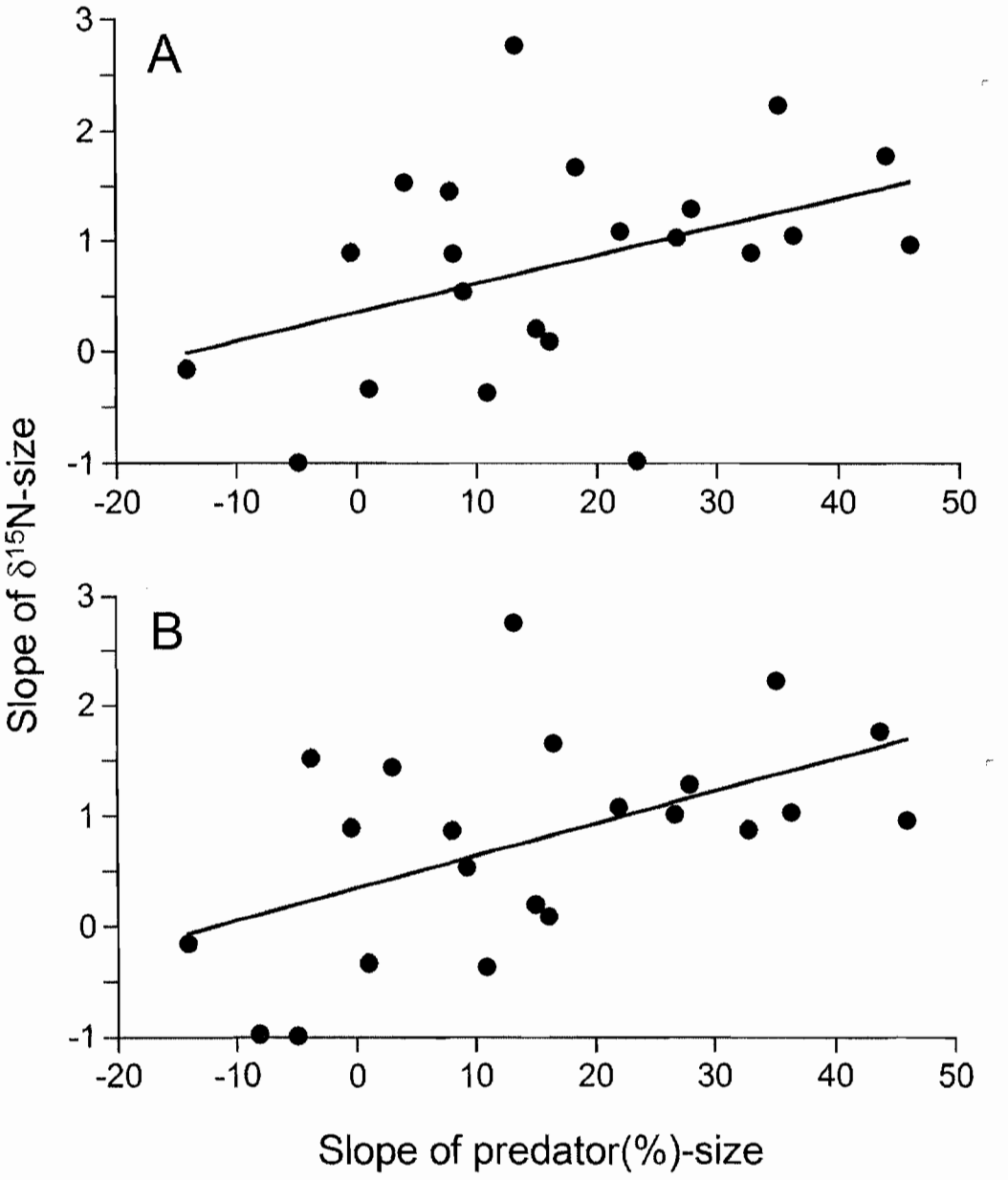
A
B
Slope of δ^{15}N-size
Slope of predator(%)-size
3
2
1
0
-1
-20
-10
0
10
20
30
40
50

Figure 4.7.

SYNTHÈSE ET CONCLUSION GÉNÉRALE

Variation spatiale du $\delta^{15}N$ des consommateurs

Le chapitre 1 a permis de démontrer que la signature isotopique des organismes aquatiques était très variable spatialement et fortement liée à la présence de charges d'azote d'origine anthropique dans le bassin versant. En effet, les charges croissantes d'azote liées aux activités anthropiques pratiquées dans le bassin versant (équivalant à une plus grande pression humaine par unité de territoire) généraient un accroissement dans le $\delta^{15}N$ des organismes aquatiques, suggérant que l'azote produit dans le bassin versant se retrouve en large partie dans les milieux aquatiques et dans les chaînes alimentaires associées. Les fumiers en particulier étaient fortement corrélés au $\delta^{15}N$, suggérant un écoulement important de ces derniers vers les milieux aquatiques. D'autres études antérieures ont observé des corrélations importantes entre la densité de bétail présente dans le bassin versant et l'écoulement de nutriments vers les milieux aquatiques (Johnes et al. 1996; Carpenter et al. 1998; Berka et al. 2001). Cet écoulement serait attribuable au fait que les grandes quantités de fumier générées par le bétail sont épandues dans les champs afin de favoriser la croissance des cultures. Or, les vastes quantités de fumier épandues dépassent souvent les besoins en nutriments des cultures ainsi que la capacité des sols à les assimiler et ces dernières s'écoulent donc librement vers les lacs et les rivières. Nos résultats appuient ces études et suggèrent que l'azote associé aux engrais produits et épandus dans les bassins versants atteint les milieux aquatiques et est assimilé dans les chaînes alimentaires aquatiques.

De plus, les résultats obtenus suggèrent que le $\delta^{15}N$ des organismes aquatiques augmente tranquillement lorsque les quantités d'azote sont faibles, mais devient de plus en plus élevé au fur et à mesure que les charges en azote croissent (relations curvilinéaires entre le $\delta^{15}N$ et les charges d'azote). Cette observation suggère que les

charges d'azote sont initialement assimilées par les plantes et les sols. Cependant, au fur et à mesure que ces charges s'élèvent, les sols deviennent saturés et les surplus d'azote sont exportés vers les milieux aquatiques. La charge d'azote à partir de laquelle le $\delta^{15}N$ se met à augmenter plus rapidement se situe vers les 300 kg N km^{-2} an^{-1}, niveau qui équivaut à des bassins versants relativement peu développés dans la présente étude (bassins versants ayant moins de 5% de leur superficie vouée à l'agriculture et/ou ayant un maximum de 19 habitants par km^2). Cette observation propose que les charges en azote produites dans un bassin versant dépassent rapidement la capacité de support du système au fur et à mesure que l'intensité des activités humaines réalisées dans un bassin versant passe d'un état faible à modéré.

En somme, ce chapitre démontre à quel point le $\delta^{15}N$ des organismes aquatiques varie d'un système à l'autre, en fonction de l'intensité des activités humaines génératrices d'azote pratiquées dans le bassin versant. Le principal constat de ce chapitre est que le $\delta^{15}N$ des organismes aquatiques peut servir d'indicateur de la perturbation du cycle de l'azote par les activités humaines à l'échelle des bassins versants. Il ne permet cependant pas de discriminer l'effet respectif des diverses sources anthropiques d'azote, celles-ci ayant acquis un $\delta^{15}N$ similaire et impossible à distinguer suite aux processus de transformation de l'azote.

Calcul de la position trophique en milieu lotique

Le chapitre 1 a démontré que le $\delta^{15}N$ des organismes lotiques est spatialement variable. Cela signifie qu'on ne peut pas comparer la position trophique d'organismes lotiques provenant de différentes localisations à partir de leur $\delta^{15}N$ brut. Il importe donc de corriger le $\delta^{15}N$ de ces consommateurs par celui d'organismes situés à la base de la chaîne alimentaire. Le chapitre 2 montre, en premier lieu, qu'il y a des différences significatives entre le $\delta^{15}N$ des différents consommateurs primaires

lotiques (situés à la base de la chaîne alimentaire), suggérant par le même fait qu'on ne peut pas utiliser n'importe quel consommateur primaire pour mesurer les positions trophiques des consommateurs supérieurs, en particulier lorsque l'on compare des positions trophiques entre plusieurs sites. Les brouteurs, qui présentent toutefois un $\delta^{15}N$ faible parmi les consommateurs primaires étudiés (qui sont donc plus herbivores que la moyenne) et qui sont bien représentés entre les sites d'étude, sont identifiés comme organisme de référence. En particulier, les Psephenidae sont choisis comme principal organisme de référence. Deux autres familles de brouteurs (Ephemerellidae et Heptageniidae) sont aussi employées dans l'élaboration du $\delta^{15}N$ de référence. Toutefois, des différences significatives sont notées entre le $\delta^{15}N$ de ces familles et les Psephenidae. Leur $\delta^{15}N$ est donc corrigé (ou ajusté) vers celui des Psephenidae, qui présentent les valeurs de $\delta^{15}N$ les plus faibles de tous les brouteurs. Ensuite, afin d'obtenir le $\delta^{15}N$ de référence final, une moyenne des valeurs de $\delta^{15}N$ de ces trois familles est réalisée pour chaque site. À partir de ce $\delta^{15}N$ de référence, la position trophique de divers organismes lotiques est finalement calculée.

Certaines différences ont été notées entre les positions trophiques des prédateurs estimées à l'aide de la méthode développée et les positions trophiques des prédateurs estimées à partir de la moyenne du $\delta^{15}N$ de tous les consommateurs primaires confondus (sans cibler les brouteurs). Bien que ces différences semblent faibles, elles proposent qu'il est préférable, lors de l'estimation de la position trophique d'organismes collectés dans différents sites d'étude, d'utiliser une quantité restreinte de taxons ayant un comportement alimentaire similaire. Si plus d'un taxon est utilisé, il peut s'avérer aussi nécessaire de corriger les différences isotopiques entre les groupes d'organismes employés afin d'uniformiser leur $\delta^{15}N$ (tel qu'effectué avec les familles de brouteurs utilisées). Ces étapes permettraient d'éviter les biais liés à l'utilisation d'organismes de référence divers ayant des $\delta^{15}N$ contrastants (collecteurs ($\delta^{15}N$ plus élevé) versus brouteurs ($\delta^{15}N$ plus faible), par exemple). Pour

conclure, le premier volet du chapitre 2 propose une méthode de sélection du $\delta^{15}N$ de référence visant à diminuer les biais engendrés par l'utilisation du $\delta^{15}N$ de n'importe quel consommateur primaire (ou n'importe quel assemblage de consommateurs primaires) lors du calcul de la position trophique des organismes lotiques. Cette méthode pourra servir d'exemple de calcul de la position trophique en milieu lotique et pourra être employée dans des études ultérieures.

Évaluation des isotopes stables de l'azote comme indicateurs de la structure des communautés

Position trophique des consommateurs

Les résultats de la présente thèse suggèrent, en premier lieu, que les isotopes stables de l'azote constituent un outil rapide et efficace de mesure de la position trophique des organismes. Ils fournissent également une information réaliste sur la position trophique des consommateurs en milieu lotique. Effectivement, les positions trophiques estimées à partir de la méthode développée dans le premier volet du chapitre 2 correspondaient assez bien aux valeurs présentées dans la littérature. Par exemple, les consommateurs primaires, les invertébrés prédateurs et les poissons se nourrissant d'invertébrés se situaient, respectivement, à 2,3, 2,9 et 3,5 niveaux trophiques, soit l'équivalent de 1,3, 1,9 et 2,5 par rapport aux producteurs primaires. Ces valeurs correspondent approximativement à celles de 1, 2 et 3 niveaux trophiques exprimées dans la littérature pour les herbivores, carnivores primaires et carnivores secondaires (Oksanen et al. 1981; Persson et al. 1992). Les positions trophiques obtenues étaient aussi comparables à celles observées dans d'autres études utilisant les isotopes stables d'azote, où les invertébrés prédateurs s'avéraient enrichis par rapport aux consommateurs primaires (Lancaster et Waldron 2001; Zah et al. 2001; Füreder et al. 2003). À un niveau taxonomique plus pointu, les estimés isotopiques

distinguaient correctement les invertébrés caractérisés dans la littérature traditionnelle comme étant des prédateurs des invertébrés non prédateurs.

Cependant, une forte variabilité dans la position trophique des invertébrés et des poissons a été observée, suggérant la présence d'omnivorie à tous les échelons du réseau trophique. Ce constat est corroboré par plusieurs études antérieures qui ont observé une variabilité importante dans le comportement alimentaire de certains taxons d'invertébrés aquatiques (Anderson 1976; Parker et Voshell 1983; Hawkins 1984; Friberg et Jacobsen 1994; Plague et al. 1998; Zah et al. 2001). Il est aussi appuyé par des études qui ont noté une importante variabilité (jusqu'à deux niveaux trophiques) dans la position trophique de poissons fourragers en lac (Vander Zanden et Rasmussen 1996; Fry et al. 1999; Vander Zanden et al. 2000). En somme, nos résultats appuient la thèse que l'omnivorie serait importante dans les milieux aquatiques.

Position trophique des poissons se nourrissant d'invertébrés comme indicateur de la structure des communautés lotiques

Bien que la position trophique des consommateurs mesurée à l'aide du $\delta^{15}N$ semble être une mesure réaliste du positionnement d'un organisme donné dans un réseau trophique, cette dernière ne semble pas être un bon indicateur de la structure de la communauté. En effet, la position trophique des poissons se nourrissant d'invertébrés a été examinée comme outil potentiel de mesure des longueurs de chaînes alimentaires. L'hypothèse initiale était que la position trophique des poissons allait refléter la structure de la communauté d'invertébrés dont ces poissons se nourrissent. Ainsi, l'apparition de prédateurs dans la chaîne alimentaire devrait allonger cette dernière, ce qui se refléterait par une position trophique plus élevée des poissons. Or, la position trophique des poissons n'était pas significativement corrélée à la présence de prédateurs dans la communauté d'invertébrés. Elle n'était pas, non

plus, reliée aux variations dans les pentes δ^{15}N-taille. Cette absence de relation suggère que la position trophique des poissons se nourrissant d'invertébrés est indépendante de la structure de la communauté d'invertébrés. En fait, la position trophique des poissons serait surtout influencée par les préférences alimentaires de ces derniers. Par exemple, les résultats suggèrent que les poissons ne se nourrissent pas nécessairement des gros invertébrés prédateurs (avec un δ^{15}N plus élevé) lorsque ces derniers sont présents. D'ailleurs, plusieurs études ont démontré que les poissons ne se nourrissent pas systématiquement des plus gros organismes disponibles, mais peuvent parfois démontrer des préférences alimentaires pour des organismes de taille moyenne, voire petite (Hansen et Wahl 1981; Teska et Behmer 1981; Bence et Murdoch 1986). Aussi, une étude effectuée en parallèle au présent doctorat et sur le même territoire d'étude a révélé que la taille moyenne des invertébrés recensés dans les estomacs des espèces de poissons utilisées dans le calcul de la position trophique était très petite (0,6 mm (taille des mailles du tamis)) comparativement au spectre total de la communauté d'invertébrés étudiée (0,5 à 8 mm (taille du tamis)). En général, les poissons se nourrissaient aussi très rarement d'organismes de grosses tailles (aucun invertébré supérieur à 3,36 mm (taille du tamis)), ce qui pourrait être dû à leur taille relativement petite (longueur corporelle totale de 68 mm en moyenne) comparativement aux gros invertébrés capturés (longueur corporelle moyenne de 21,5 mm pour les organismes du plus gros tamis (8 mm)). La principale conclusion de ce volet est donc que la position trophique des poissons ne semble pas être un indicateur efficace de la structure des communautés, celle-ci étant trop influencée par le comportement alimentaire des poissons.

Relations δ^{15}N-taille de la communauté d'invertébrés

Les relations δ^{15}N-taille des communautés d'invertébrés pourraient potentiellement servir d'indicateurs de la structure des communautés lotiques. En effet, les pentes δ^{15}N-taille augmentaient de façon significative avec l'augmentation

de la proportion de prédateurs en fonction de la taille (pentes pourcentage de prédateurs-taille plus élevées; excluant les sangsues, qui sont plus tolérantes à la pollution). Une telle augmentation du $\delta^{15}N$ avec l'augmentation de la proportion de prédateurs est prévisible, puisque les prédateurs ont un $\delta^{15}N$ typiquement plus élevé que leurs proies (France et al. 1998; Lancaster et Waldron 2001; Anderson et Cabana 2007). Ce constat suggère que les pentes $\delta^{15}N$-taille répondent aux changements dans la proportion de prédateurs dans les diverses classes de taille de la communauté et, conséquemment, qu'elles reflètent les changements dans la structure trophique des communautés. C'est pourquoi nous les proposons en tant qu'indicateurs de la structure des communautés lotiques.

Impact de facteurs environnementaux et anthropiques sur la structure des communautés aquatiques

Deux propriétés liées à la structure des communautés ont été examinées dans le cadre de cette thèse, soit la densité et la longueur de la chaîne alimentaire mesurée à l'aide des isotopes stables de l'azote.

Densité des communautés d'invertébrés lotiques

Dans le chapitre 3, nous avons employé trois variables liées à des processus ascendants afin de prédire la densité des invertébrés lotiques. La productivité, première variable examinée, expliquait seulement une fraction de la variabilité dans la densité de certaines classes de taille étudiées. En particulier, la densité de deux des plus grosses classes de taille était plus grande lorsque les concentrations de chlorophylle *a* étaient plus élevées. Toutefois, ni la température, ni la position trophique (les deux autres variables ascendantes étudiées) n'expliquaient de façon significative les variations dans la densité des diverses classes de taille examinées. À l'aide d'une régression multiple portant sur la totalité des classes de taille et des sites

étudiés, nous avons trouvé que la taille des organismes expliquait 47% de la densité des invertébrés. Effectivement, les invertébrés de petite taille étaient significativement plus abondants que les gros organismes. La chlorophylle *a* et l'azote contribuaient, quant à eux, à expliquer 9% de plus de la variation dans la densité, pour un total de 56% (régression multiple).

Plusieurs études ont observé un effet déterminant de la taille des organismes sur leur densité (Damuth 1981; Peters et Raelson 1984; Cyr et al. 1997a). En milieu aquatique, Damuth (1987) et Cyr et al. (1997a) ont noté une forte relation inverse entre la densité et la taille des organismes (r^2 de 0,81 et 0,92 respectivement). Ces coefficients étaient plus élevés que ceux obtenus dans la présente étude et pourraient être dus au fait que l'intervalle de taille examiné par ces deux études antérieures était beaucoup plus grand que celui que nous avons employé. D'ailleurs, d'autres études employant un intervalle de taille comparable à celui que nous avons utilisé ont obtenu des coefficients de détermination semblables aux nôtres (r^2 de 46 à 51%; Schmid et al. 2000; Solimini et al. 2001).

De nombreuses études réalisées en milieu aquatique ont également noté un accroissement de la densité des organismes en fonction de la productivité du milieu (Hart et Robinson 1990; Bourassa et Morin 1995; Perrin et Richardson 1997). En particulier, Cyr et al. (1997b) ont observé un accroissement plus rapide dans la densité des petits organismes en fonction de la productivité, par rapport aux gros organismes. Or, nous avons constaté un accroissement significatif de la densité en fonction de la productivité seulement auprès de deux grandes classes de taille. Encore une fois, cependant, l'intervalle de taille utilisé dans l'étude de Cyr et al. (1997b) était plus grand que le nôtre et pourrait être responsable de la divergence des résultats. D'ailleurs, Bourassa et Morin (1995), dont l'étude ciblait des invertébrés aquatiques, ont observé des résultats similaires aux nôtres. Ils ont noté un accroissement plus rapide de l'abondance des gros organismes comparativement aux petits organismes

dans les sites productifs. Ce constat – que seule la densité des gros organismes semble influencée par la productivité dans la présente étude – n'appuie pas certaines de nos hypothèses initiales telles que :

1) La densité des petits organismes, qui présentent des taux de croissance plus rapides que les gros organismes (Hennemann 1983; Gillooly et al. 2001; Savage et al. 2004), devrait croître plus rapidement dans les sites productifs et chauds que la densité des gros organismes.

2) L'accroissement de la densité des gros organismes devrait être moins rapide que celle des petits organismes dans les sites productifs à cause de la diminution de l'efficacité de transfert énergétique lorsqu'on s'élève dans la chaîne alimentaire (les organismes plus gros étant souvent des prédateurs).

Nos résultats appuient plutôt les hypothèses suivantes :

1) Les systèmes productifs fournissent de plus grandes quantités de nourriture, ce qui aurait pour effet de favoriser la croissance et d'augmenter la taille moyenne des organismes.

2) La présence de cascades trophiques descendantes pourrait générer de plus grandes densités de gros organismes dans les sites productifs, par rapport aux petits organismes (Fretwell 1977; Arruda 1979; Oksanen et al. 1981). En effet, une plus grande productivité à la base de la chaîne alimentaire pourrait profiter aux prédateurs (organismes plus gros) en augmentant la quantité de proies. Cette augmentation élèverait à son tour la densité des prédateurs, qui contrôleraient ensuite la densité des plus petits organismes, soit leurs proies. Ceci aurait pour effet de stabiliser la densité des petits organismes (consommés par les plus gros). Conséquemment, la densité des gros organismes augmenterait parallèlement à la productivité, tandis que la densité des petits organismes demeurerait similaire.

Certaines études antérieures ont documenté un accroissement de la productivité des invertébrés aquatiques dans les milieux plus chauds (Plante et Downing 1989; Morin et Bourassa 1992), ainsi que de plus fortes densités de certains organismes dans des milieux réchauffés par des effluents de centrales thermiques (Hellawell 1986). Bien que les températures annuelles de l'eau mesurées dans les sites examinés dans la présente étude variaient entre 6 to 15 °C, nous n'avons observé aucun effet significatif de la température sur la densité. De façon similaire, aucune relation significative n'a été recensée entre la densité et la position trophique des organismes constituant une classe de taille donnée. Dans une étude récente, Cohen et al. (2003) conclurent que la position trophique des organismes expliquait une partie de la variation dans leur abondance. Toutefois, la position trophique expliquait une part beaucoup moins importante de la variabilité dans l'abondance des organismes que la taille de ces derniers. De plus, la position trophique était généralement associée à des changements dans la taille et Cohen et al. (2003) n'examinèrent pas l'effet de la position trophique sur la densité de classes de taille individuelles.

En somme, outre la taille des organismes, les variables utilisées expliquaient seulement une très faible proportion de la variabilité dans la densité des organismes. Il est possible que les facteurs descendants (prédation), ou encore l'effet de la pollution (diminution de la densité d'espèces intolérantes, mais accroissement de la densité d'espèces tolérantes), jouent des rôles plus importants sur la densité des organismes en milieu lotique que les facteurs ascendants examinés.

Longueur des chaînes alimentaires

Les résultats obtenus suggèrent que les activités anthropiques qui accroissent la productivité et les concentrations de contaminants (perturbations) dans les milieux aquatiques altèrent les chaînes alimentaires lotiques. Une des mesures liées à la longueur de chaîne alimentaire, soit la pente δ^{15}N-taille, était plus faible dans les

milieux perturbés par des activités industrielles et plus élevée dans les sites productifs, suggérant une chaîne plus courte dans les milieux perturbés et plus longue dans les milieux productifs. D'autres études ont observé des résultats similaires aux nôtres. Par exemple, plusieurs études traditionnelles (n'employant pas les isotopes stables d'azote pour estimer les longueurs de chaînes) ont noté un effet significatif de la productivité sur l'allongement des chaînes alimentaires (Jenkins et al. 1992; Townsend et al. 1998; Thompson et Townsend 2005). Au niveau des études isotopiques existantes, Vander Zanden et al. (1999a) ont également observé un effet positif significatif, quoique modeste (36% de la variation expliquée), de la productivité (profondeur de disque Secchi) sur la position trophique du touladi (*Salvelinus namaycush*). Pour ce qui est de l'effet des activités industrielles sur les chaînes alimentaires, Sherwood et al. (2002) ont trouvé que les chaînes alimentaires des lacs pollués par des métaux lourds étaient simplifiées, ce qui affectait le développement des perchaudes (*Perca flavescens*) présentes dans ces lacs. La présente étude complémente ces études antérieures en examinant l'effet simultané de variables liées à la productivité et aux perturbations sur la longueur des chaînes alimentaires dans des sites touchés de façon plus ou moins intense par diverses activités humaines.

La variabilité dans les pentes δ^{15}N-taille pourrait s'expliquer par différents phénomènes. Premièrement, maintes études ont démontré que certains gros prédateurs, dont plusieurs sont communs dans les sites examinés dans le cadre de la présente étude, sont intolérants à la pollution d'origine humaine (Resh et al. 1996; Pelletier et St-Onge 1998; Pelletier 2002; Voshell 2002). La disparition de ces derniers des sites perturbés pourrait donc contribuer à l'affaiblissement des pentes δ^{15}N-taille. À l'inverse, une productivité accrue pourrait soutenir des quantités croissantes de gros prédateurs, en fournissant plus d'énergie à la base de la chaîne alimentaire (Lindeman 1942; Fretwell 1977; Oksanen et al. 1981). Une augmentation

dans la proportion des gros prédateurs aurait ensuite pour effet d'élever les pentes δ^{15}N-taille (les prédateurs ayant un δ^{15}N plus élevé), ce qui expliquerait la relation observée.

Fait intéressant, une plus grande proportion de la variabilité dans les pentes δ^{15}N-taille était expliquée lorsque la productivité (chlorophylle *a*) et les perturbations (nombre d'industries) étaient utilisées simultanément. Ceci suggère que ces deux variables présentent des intensités variables entre les sites d'étude et s'avèrent parfois entremêlées. Conséquemment, l'effet de l'une tendrait à obscurcir l'effet de l'autre. Toutefois, au total, il est possible de conclure que la productivité tend à accroître la longueur des chaînes alimentaires (via les pentes δ^{15}N-taille), tandis que les activités industrielles pratiquées dans le bassin versant tendent à la diminuer.

En somme, le chapitre 4 suggère que les pentes δ^{15}N-taille fournissent une information valable sur la structure des communautés et sur l'altération de ces dernières par les activités anthropiques.

Limites de la méthode isotopique

Les isotopes stables de l'azote permettent d'estimer rapidement la position trophique des organismes et offrent des informations sur certaines caractéristiques trophiques des chaînes alimentaires. Toutefois, plusieurs études remettent en question l'utilisation d'une valeur unique de fractionnement (3,4‰, par exemple) lors du calcul de la position trophique de divers types d'organismes (Vander Zanden et Rasmussen 2001; McCutchan et al. 2003; Vanderklift et Ponsard 2003). Dans la présente étude, une seule valeur de fractionnement, soit 3,4‰ (Minagawa et Wada 1984; Post 2002b), a été employée afin d'estimer la position trophique des organismes lotiques. Conséquemment, une partie de la variabilité perçue dans la

position trophique des organismes, que l'on avait jusqu'à maintenant attribuée à la présence d'omnivorie (chapitre 2 en particulier), pourrait être liée à la présence d'un fractionnement variable entre les organismes étudiés. À titre d'exemple, Jardine et al. (2005) ont noté un fractionnement variable du ^{15}N entre différents groupes fonctionnels d'invertébrés capturés en rivière. Ils ont aussi observé un fractionnement variable chez différentes familles d'invertébrés en fonction de la qualité de la diète et ont suggéré que ceci pouvait mener à une variabilité spatiale dans la position trophique d'un même organisme. Malgré ces interrogations, les positions trophiques mesurées dans le cadre du présent document correspondaient, de façon générale, à celles présentées dans la littérature. Ceci suggère que les positions trophiques calculées à l'aide des isotopes stables d'azote permettent de dépeindre un portrait réaliste du comportement alimentaire des organismes. Ces dernières distinguaient effectivement bien les organismes herbivores des organismes carnivores. Il importe toutefois de garder en tête qu'il ne faut pas tirer de conclusions hâtives quant à la variabilité de la position trophique d'un groupe donné d'organismes, cette dernière pouvant être partiellement attribuable à l'omnivorie, mais également au fractionnement variable du ^{15}N chez les organismes.

Conclusion

L'approche générale présentée dans cette thèse consistait à utiliser des mesures basées sur le $\delta^{15}N$ des organismes lotiques afin d'évaluer si et comment celles-ci peuvent refléter différents types de perturbations d'origine anthropique. Les principaux constats sont :

1) Le $\delta^{15}N$ des organismes aquatiques collectés en rivière est spatialement très variable et fortement associé aux sources d'azote anthropique à l'échelle du bassin versant. Il peut donc servir d'indicateur des perturbations anthropiques du cycle de l'azote au sein des bassins versants.

2) Le $\delta^{15}N$ est également variable entre les divers organismes situés à la base de la chaîne alimentaire lotique pour un site donné. Il est conséquemment préférable, lors de l'estimation de la position trophique des consommateurs collectés dans différents sites d'étude, d'utiliser une quantité restreinte de taxons ayant un comportement alimentaire comparable.
3) La position trophique des organismes lotiques établie à l'aide des isotopes d'azote semble refléter de façon réaliste le comportement alimentaire de ces derniers (distinction des herbivores versus carnivores, par exemple).
4) La position trophique des poissons se nourrissant d'invertébrés n'est cependant pas un bon indicateur de la structure des communautés, étant possiblement trop influencée par le comportement alimentaire (préférences) de ces derniers.
5) La pente $\delta^{15}N$-taille de la communauté d'invertébrés semble être un indicateur adéquat de l'impact des activités humaines (productivité et perturbation) sur la structure trophique des communautés lotiques. Elle pourrait être utilisée en complémentarité avec les indices d'intégrité biotiques qui ciblent davantage l'effet des perturbations sur les espèces particulières que sur les communautés entières (chaîne alimentaire).
6) La densité des communautés d'invertébrés en entier est fortement associée à a taille des organismes (plus grande densité chez les petits organismes). La variation dans la densité des invertébrés lotiques à l'intérieur des classes de taille est cependant peu expliquée par les facteurs ascendants tels que la productivité, la température ou la position trophique mesurée à l'aide des isotopes stables d'azote.

Pour conclure, la présente étude démontre l'utilité des isotopes stables de l'azote dans les études écosystémiques. D'une part, ils s'avèrent de bons indicateurs de la présence d'azote d'origine anthropique dans les cours d'eau et de la perturbation

du cycle de l'azote par les activités anthropiques à l'échelle des bassins versants. D'autre part, ils offrent aussi des informations sur le comportement alimentaire des organismes et leur position dans les réseaux trophiques. Finalement, ils permettent de décrire, dans une certaine mesure, la structure trophique des chaînes alimentaires (en particulier pour ce qui est des pentes δ^{15}N-taille) et comment celles-ci répondent à différentes perturbations environnementales et anthropiques. Ces résultats ont des implications majeures pour les études futures, qui pourront se servir des isotopes stables d'azote comme mesure rapide et complémentaire de la structure des communautés et de l'altération des écosystèmes aquatiques par les activités humaines. En outre, quelques mesures de δ^{15}N sur des consommateurs bien choisis permettront d'obtenir un portrait rapide et global de l'intensité des activités humaines génératrices d'azote pratiquées sur le bassin versant, ainsi que du comportement alimentaire des consommateurs et de l'état de la chaîne alimentaire à laquelle ils appartiennent.

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